Parasites of the past: 90 years of change in parasitism for English sole

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Historical data are extremely rare but essential for ascertaining whether contemporary infectious disease burdens are unusual. Natural history collections are a valuable source of such data, especially for reconstructing long timelines of parasite abundance. We quantified the parasites of 109 museum specimens of English sole (*Parophrys vetulus*), an economically important flatfish, collected from Puget Sound, Washington, over a 90-year period (1930–2019). We counted nearly 2,500 individual parasites representing 23 distinct species/morphotypes and four broad taxonomic groupings. Of the 12 taxa that were prevalent enough to include in the analysis, nine did not change in abundance over time, two (an acanthocephalan and a trematode) decreased, and one (another trematode) increased. By broad taxonomic grouping, nematodes, trematodes, and leeches exhibited no change over time, whereas acanthocephalans declined significantly. The diverging patterns among parasite taxa suggest a double-edged sword of responses to long-term ocean change: some parasites might be on the rise, while others are declining.

Outbreaks of marine disease are an increasingly common occurrence worldwide; urchins in the Caribbean (Lessios 1988), abalone in California (Lafferty and Kuris 1993), and sea stars on the west coast of North America (Hewson *et al.* 2014) have experienced recent epidemics resulting in mass mortality. Although the underlying causes have not been conclusively identified, such outbreaks are often attributed to climate change (Harvell *et al.* 2002) or ongoing marine biodiversity loss (Lafferty and Kuris 1993). This apparent uptick in infection has led some disease ecologists to conclude that the oceans face a

"rising tide" – that is, an unprecedented increase – of marine parasitism (Hayes *et al.* 2001; Harvell *et al.* 2004).

At the same time, parasitologists and ecologists warn of the possibility that parasite species are being driven to extinction at unprecedented rates (Stork and Lyal 1993). Parasites cannot exist without hosts, and the loss of marine species diversity could therefore lead to loss of parasites (Dunn *et al.* 2009); several researchers have even posited that co-extinction of parasites could in fact be the most common form of biodiversity loss (Dougherty *et al.* 2016). The most susceptible parasites are likely those that require multiple hosts to complete their life cycles (Wood *et al.* 2014). Climate change is also implicated in the predicted declines in parasite species, with parasites that have high host specificity, complex life cycles, and narrow thermal tolerance ranges at greatest risk (Carlson *et al.* 2017).

Understanding whether oceans are experiencing an uptick in levels of infection or undergoing an invisible wave of parasite extinction is critical for marine resource management. Parasites are ecologically influential and changes in their abundance could have ripple effects throughout ocean ecosystems. On the one hand, an increase of marine diseases could result in disease-driven declines of host species that are valuable to fisheries or that contribute to ecosystem integrity, while on the other hand, a loss of parasite species could translate into a corresponding loss of the ecological functions performed by those species (eg Hatcher *et al.* 2012). Given the substantial ecological influence of parasites (Wood and Johnson 2015), there is an urgent need for research on how parasite abundance has changed over time.

Despite increasing calls by ecologists for long-term data on the burden of marine infectious diseases, few such datasets exist (Aguirre-Macedo *et al.* 2011; May-Tec *et al.* 2013); only a handful of empirical studies have measured marine parasite burden over timespans longer than a decade (Howard *et al.*

In a nutshell:

- Marine ecosystems have changed considerably over the past century, raising the question of whether levels of infectious disease observed today are "normal" in a historical context

- Historical data on parasites over a century-long timescale can be extracted from examination of fluid-preserved fishes maintained in natural history collections

- Among parasites of English sole (*Parophrys vetulus*) collected during 1930–2019 from Puget Sound, Washington, disease trajectories were complex and variable, with some parasites increasing in abundance over time and others declining

- Parasite responses to environmental change appear idiosyncratic among taxa, and predictions for future change might need to be host-, parasite-, and locality-specific

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2019). In one example, over a 12-year period, Grutter *et al.* (2019) measured change in coral reef fish ectoparasite loads in response to fish population abundance on Australia's Great Barrier Reef. Other studies have relied on disjunct temporal observations to make inferences about change over time; for instance, analysis of two collections of estuarine fishes, one performed in ~1971 and the other in ~2000, revealed that more than half of the parasite taxa detected in these hosts declined in abundance over that 30-year period (Olson *et al.* 2004).

Meta-analyses have also been used to characterize long-term change in marine infection (Ward and Lafferty 2004; Fiorenza *et al.* 2020a), but such analyses also have shortcomings. Meta-analyses typically extend back only several decades, to the publication dates of the earliest papers systematically catalogued in research databases. They can also be biased by the "file drawer" problem, in which null results are rarely reported in the literature, and increasing interest in an infectious disease can drive observed patterns (Fey *et al.* 2015). To conclusively determine whether rates of marine disease are changing over time, scientists will need primary, empirical data collected over many decades.

Parasitological dissection of natural history specimens could fill this research gap (Harmon *et al.* 2019). Such holdings contain millions of preserved fish collected over the past few centuries, and parasites that infected these fish in life are often also preserved with morphological integrity within their hosts (Fiorenza *et al.* 2020b). For example, Black (1983) used museum specimens to demonstrate that lake trout (*Salvelinus namaycush*) in the North American Great Lakes lost a parasitic nematode (*Cystidicola stigmatura*) when the trout population crashed in 1925. Although this approach has been validated (Fiorenza *et al.* 2020b), it has not been used to reconstruct a trajectory of change for a suite of parasite species – a missed opportunity to examine whether ecosystems are indeed facing a "rising tide" of marine disease.

We addressed this gap in the historical record by generating primary data on the dynamics of marine parasitism over a nine-decade period within one region, using parasitological dissection of fluid-preserved museum specimens. We reconstructed historical parasite assemblages of English sole (*Parophrys vetulus*) collected from Puget Sound, Washington, between 1930 and 2019 by identifying and counting parasites preserved in sole stored in natural history collections. We chose English sole because it is among the most abundant benthic fish species in Puget Sound (Toft *et al.* 2007) and is well represented in US natural history collections across the 20th century (www.fishnet2.net). We sought to answer two questions: (1) what is the trajectory of change over time for each of the parasite taxa detected, and (2) are parasites that use multiple host species over the course of their life cycles more likely to decline over time than directly transmitted parasites?

▮ Methods

Specimen selection and collection site history

We focused on the metazoan parasites of Puget Sound English sole collected over the period 1930–2019 (Figure 1). Puget Sound is the second-largest estuary in the world, and 93.5% of the Sound's shoreline has been anthropogenically modified since the 1850s (Simenstad *et al.* 2011). From 1917 to the 1950s, English sole of this region were targeted in a high-value commercial fishery, and peak catch rate occurred in the late 1950s (reviewed in Stewart [2005]). At present, Puget Sound English sole are indirectly protected from overfishing by both groundfish management plans designed to protect other species (Stewart 2005) and regional and complete trawling bans, implementation of which began in 1989 and 1994, respectively (Palsson *et al.* 2009).

We sourced English sole specimens from the University of Washington's Burke Museum Ichthyology Collection (hereafter, University of Washington Fish Collection, UWFC; WebPanel 1). We aimed for our subsample of specimens to match the average size of English sole in the UWFC (UWFC, mean total length [TL] ± standard deviation [SD] = 164.480 ± 53.294 mm; this study, mean TL ± SD = 165.101 ± 42.146 mm), and included fish collected from a diversity of localities within Puget Sound. Our goal was to survey 14 fish from each decade to (1) obtain similar sample sizes across the nine available decades and (2) dissect the maximum allowable number of fish while still allowing the majority of UWFC's English sole holdings to remain undissected, thereby ensuring availability of intact specimens for future museum loans (goal of $n = 125$, 41% of the Puget Sound English sole specimens and 6% of the total number of English sole specimens in the overall UWFC). Five decades had fewer than 14 specimens (1950: $n = 6$; 1960: $n = 8$; 1970: $n = 11$; 1980: $n = 13$; 1990: $n = 13$), and one decade had 16 specimens (2000). Therefore our total sample size was 109 specimens.

Parasitological dissection

Each fish was subjected to a comprehensive parasitological dissection (detailed in WebPanel 1). For each parasite identified, we noted its broad taxonomic grouping (Subclass Copepoda, Subclass Hirudinea, Class Trematoda, Class Cestoda, Phylum Nematoda, Phylum Acanthocephala). If multiple parasite taxa of a single genus or grouping were identified, they were each assigned a unique identifier (for instance, "sp 1", "sp 2"). Each broad taxonomic grouping was classified into one of two transmission strategies: directly transmitted (using one host species over the course of the life cycle) or complex (using multiple host species over the course of the life cycle). Parasites were accessioned into the Harold W Manter Laboratory of Parasitology at the University of Nebraska-Lincoln and can be traced back to their host by the UWFC catalog number.

Statistical analyses

All statistical analyses were performed with R (v3.6.1; R Core Team 2019). Individual analyses are discussed below; explanations for temporal and spatial autocorrelation assessments, tests, and the functions and packages used are provided in WebPanel 2. All scripts and files associated with this study are available on our Github repository: https://github.com/wood-lab/Welicky-et-al.-2021-Frontiers-Ecol-Environ.

Detecting change over time in the abundance of individual parasite taxa

To determine whether parasite abundance changed over the period 1930–2019 for each parasite taxon detected, we examined the relationship between parasite abundance and collection year using generalized linear mixed models with a negative binomial error distribution. These analyses were performed only for parasites with >5% prevalence because analyses of parasite taxa with fewer detections would have had low statistical power. "Prevalence" was defined as the proportion (percent) of fish infected with a given parasite taxon (Bush *et al.* 1997). Parasite abundance (ie number of parasites of that taxon per host; Bush *et al.* 1997) was the response variable, and year of collection was the fixed effect. Because fish size and parasite abundance are positively correlated (Poulin 1999), we offset the response variable using the log of fish standard length to control for host size. Site was included as a categorical random effect in the model.

Detecting change over time in the number of parasite individuals within each broad parasite taxonomic group and transmission strategy

We were interested in determining whether species-level changes were consistent within broad taxonomic groupings; that is, we wanted to test whether the direction and magnitude of change over time in the number of complex life-cycle parasites differed from that of directly transmitted parasites. We used the results obtained from the aforementioned individual species models to test these hypotheses. Parasites were divided into five broad taxonomic groupings: Hirudinea, Copepoda, Trematoda, Nematoda, and Acanthocephala. The Cestoda were excluded because their prevalence was <5%. The estimate and standard error of the Acanthocephala were derived from a single model that grouped species that could not be separated by morphotype. Transmission strategy was classified into two levels: direct or complex. For each of these factors, we employed a meta-regression model where effect size estimates were the regression coefficients for the effect
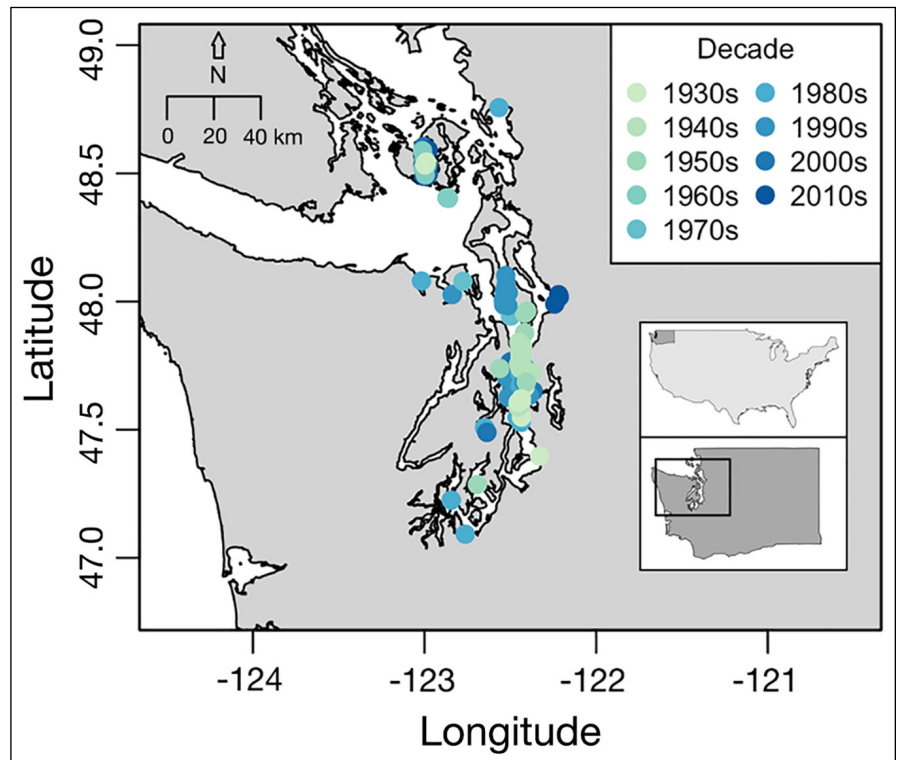

Figure 1. Map of Puget Sound, Washington. Data points represent sites where specimens of English sole were collected.

of year on abundance of each parasite (after Wood *et al.* 2014).

■ Results

A total of 2,450 parasite individuals were detected in 109 preserved English sole specimens. These parasites represented 23 distinct species/morphotypes and four groups of parasites that were identified into broad taxonomic groupings but could not be fully taxonomically resolved. Of the total number of parasite individuals counted, 82.41% were nematodes, 13.22% were trematodes, 1.63% were acanthocephalans, 1.35% were cestodes, 0.74% were leeches, and 0.65% were crustaceans. Nearly 90% of fish were infected with at least one species of nematode, 41.28% with at least one species of trematode, 18.35% with at least one species of acanthocephalan, 9.17% with at least one species of crustacean, 9.17% with at least one species of leech, and 1.84% with at least one species of cestode. Twelve parasite taxa exceeded 5% prevalence (WebTable 1).

Change over time in abundance of individual parasite taxa

Nine of the 12 parasite taxa did not change significantly in abundance over time. The larval trematode, metacercaria sp 2, increased in prevalence over time, and the acanthocephalan *Echinorhynchus* spp and adult trematode Opecoelidae sp 1 decreased in abundance over time (Figure 2; WebTable 2).
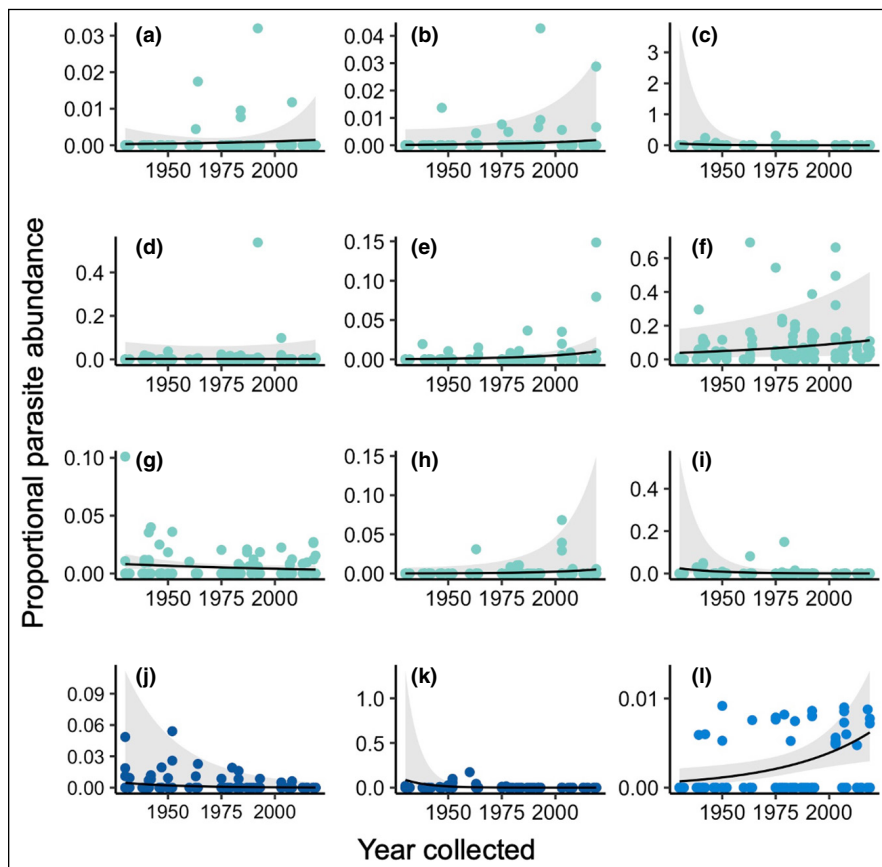
Figure 2. Change in abundance over time for parasites with >5% prevalence. The y-axis is proportional parasite abundance (predicted number of parasites per millimeter of fish length). The predicted fit of the generalized linear mixed model is depicted by the solid black line and the 95% confidence interval is depicted by the gray band. Data points are the raw data representing abundance adjusted for host length for each individual. Green dots indicate models that were $P > 0.05$; navy and bright blue dots indicate models that were significantly declining or increasing ($P < 0.05$), respectively. (a) Copepoda sp, (b) *Oceanobdella pallida*, (c) Trematoda sp 3, (d) metacercaria sp 1, (e) *Clavinema mariae*, (f) *Cucullanus annulatus*, (g) *Contracaecum* sp, (h) *Capillaria parophysi*, (i) Spirurida sp 1, (j) *Echinorhynchus* spp, (k) Opecoelidae sp 1, (l) metacercaria sp 2.

Change over time in number of parasite individuals within each broad parasite taxonomic group and transmission strategy

Across all five broad taxonomic groupings, there was no significant change in abundance over time (estimate = + 0.003, standard error [SE] = 0.003, z = 0.921, P = 0.357; Figure 3). Within the five broad taxonomic groupings, the Acanthocephala declined in number over time, and no other groups changed significantly (Figure 3; Table 1). Transmission strategy was not a significant predictor of the direction of change in the number of parasite individuals over time (Figure 3; Table 1).

◼ Discussion

Of the 12 parasite taxa examined, 25% exhibited significant change: a larval trematode, metacercaria sp 2, increased in presence over time, and the acanthocephalan *Echinorhynchus*

spp and adult trematode Opecoelidae sp 1 decreased in abundance over time. Of the broader taxonomic groupings, only the Acanthocephala declined in abundance from 1930 to 2019. Parasite transmission strategy was not a significant predictor of change in abundance over time. The diverse responses of parasites to environmental change over the past 90 years suggest that the oceans face neither an increase in infectious disease nor an invisible wave of parasite extinctions in this host–parasite system; instead, our data suggest that the responses of parasites to long-term change in environmental conditions are likely to vary across parasite taxa.

No evidence of change through time was found for nine of the 12 parasite taxa. This could be because they did not change through time or possibly because we lacked the statistical power to detect temporal change. Even in studies with high statistical power, many parasite taxa are resilient to major ecological changes (Wood *et al.* 2014, 2015). However, our statistical power was limited by the number of specimens available in natural history collections for destructive sampling and might have prevented us from detecting some changes that would be detectable with greater replication. For example, our research group recently reported an eight-fold increase in the abundance of a parasitic marine nematode (*Clavinema mariae*) between 1930 and 2016 (Howard *et al.* 2019), yet here we observed merely a consistent but non-significant increase in the abundance of this nematode species. After comparing our datasets and analyses, we concluded that the divergent results were due to differences in sample size between our study (n = 109) and that of Howard *et al.* (2019; n = 307), who were able to examine every specimen of Puget Sound English sole in the UWFC because this nematode can be counted without the need for destructive sampling. For our study, destructive sampling precluded access to a larger sample size, which may have limited our ability to detect more subtle or nuanced changes through time.

Our experimental design did not allow us to determine the specific drivers of change in abundance or presence for the three taxa where change was detected. However, we can offer some testable hypotheses that are consistent with the evidence presented here. For example, the rise of metacercaria sp 2 could be explained by changes in conditions linked to broader changes in climate. Local average annual sea-surface temperatures have increased by 1°C over the 90-year study period (Snover *et al.* 2005), and higher water temperature has been shown to facilitate parasite populations by enhancing parasite development rate (Kamiso and Olson 1986; Lõhmus and

Björklund 2015), reducing generation time (Groner *et al.* 2014), and lengthening the reproductive season (Altizer *et al.* 2013). Alternatively, the rise of this parasite might be indirectly driven by greater nutrient input into Puget Sound, as this could promote increases in the abundance of intermediate host snails (Kalinda *et al.* 2017). However, we find the climate hypothesis more compelling than the nutrient hypothesis, given that terrestrial and soil organic matter input into Puget Sound peaked in the 1960s due to the 1972 passage of the US Clean Water Act. Nutrients could still remain a plausible explanation for increasing parasite abundance if pollution caused intermediate host populations to tip into an alternate stable state from which the ecosystem has yet to recover.

We also hypothesize that host density and host health could play a role in facilitating parasite transmission. Greater host abundance increases the encounter rate between hosts and parasites, which enhances transmission and overall parasite abundance (eg Bagge *et al.* 2004). English sole serve as either intermediate or definitive hosts for the parasite taxa we detected. Their populations have not experienced a unidirectional change in abundance and have remained relatively stable over the time frame of this study. Since 1982, the stability of English sole populations in Puget Sound have been linked with management plans that directly and indirectly reduced fishing (Pedersen and DiDonato 1982; Palsson *et al.* 2009). If host density is a primary control of parasite abundance, then the lack of change observed in parasite abundances is unsurprising.
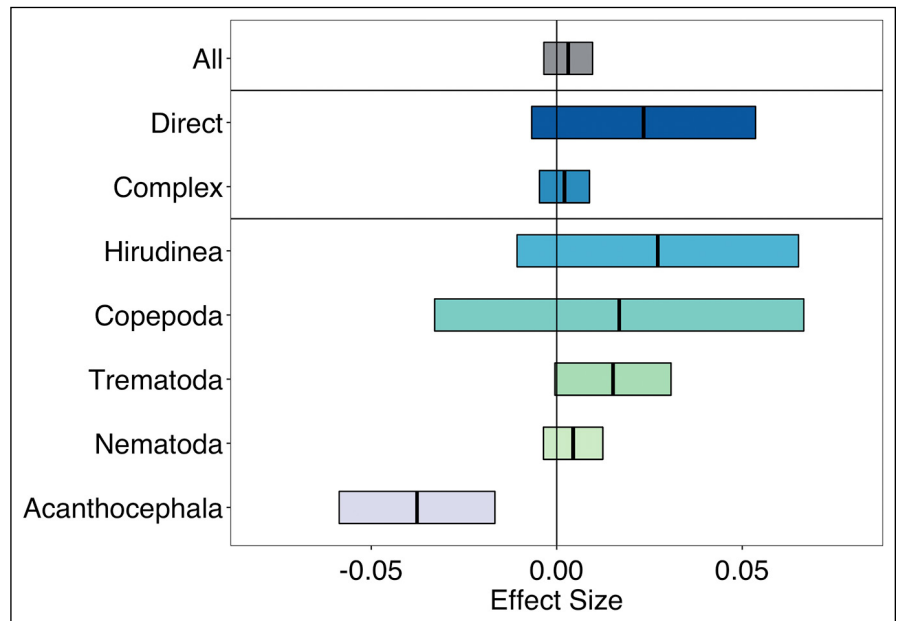

Figure 3. Meta-regression estimates for the effects of year on mean parasite abundance by life-cycle type and parasite group. Estimates of the effect sizes were derived from meta-regression models testing whether there is an overall effect of the year on parasite abundance. Positive values indicate increasing abundance and negative values indicate decreasing abundance. Estimates are shown with 95% confidence intervals.

Because English sole population size is not a likely explanation for the observed significant change in abundance of the three parasite taxa, host condition should be considered (eg Myers *et al.* 1987; Malins *et al.* 1996). Groundfishes have been exposed to numerous pollutants over the past 90 years, leaving English sole immunocompromised (eg Myers *et al.* 1990; Malins *et al.* 2006). In fact, this species is used as a sentinel in pollutant monitoring, because of their abundance and susceptibility to pollution-driven physiological abnormalities

Table 1. Results of the meta-regression analyses examining the effects of time on abundance for taxonomic grouping and life-cycle transmission strategy

	Estimate	SE	z	P	ci.lb	ci.ub
Taxonomic grouping *Test of moderators* Q_m (df = 5) = 19.5716, P = 0.002						
Acanthocephala	−0.038	0.011	−3.516	0.000	−0.059	−0.017
Copepoda	0.017	0.025	0.663	0.507	−0.033	0.067
Hirudinea	0.027	0.019	1.407	0.159	−0.011	0.065
Nematoda	0.004	0.004	1.083	0.279	−0.004	0.012
Trematoda	0.015	0.008	1.901	0.057	−0.001	0.031
Life-cycle transmission strategy *Test of moderators* Q_m (df = 2) = 2.679, P = 0.262						
Complex	0.000	0.003	0.605	0.545	−0.005	0.009
Direct	0.023	0.015	1.521	0.128	−0.007	0.054

Notes: Q_m = omnibus test for between-group heterogeneity; df = degrees of freedom; SE = standard error; ci.lb = confidence interval lower bound; ci.ub = confidence interval upper bound.

(Johnson *et al.* 2013). Although mitigation efforts to limit pollutant inputs are currently in place (eg Ginn and Pastorok 2018), English sole remain affected by past and present pollution (eg West *et al.* 2017). Perhaps the interaction between host availability and reduced host immunity has benefited generalist parasites (eg metacercaria sp 2) by rendering the available hosts more susceptible to infection (eg Rohlenová *et al.* 2011).

For the two parasite taxa that have declined through time, two drivers could be important: reduction in host abundances and the direct effects of environmental change on parasites. Fishing can reduce the abundance (Wood *et al.* 2014) and diversity (Wood and Lafferty 2015) of complex life-cycle parasites by removing obligate hosts from the ecosystem. Complex life-cycle parasites are especially prone to decline as a consequence of fishing-driven biodiversity loss due to the greater likelihood that one of their required hosts will be lost (Wood *et al.* 2010). Over the study period, English sole density has remained relatively stable, but other required hosts may have declined. There are few top predators of adult English sole, one being the bluntnose sixgill shark (*Hexanchus griseus*); fishing of this shark has been prohibited since 2001 because the species is data deficient and population information is scarce (King *et al.* 2017). Therefore, top-down control of parasites that use English sole as an intermediate host may be occurring due to increased predation. Parasites may also be declining in overall abundance if the body size of English sole and/or other hosts they infest are smaller today than in the past, as host size and parasite intensity are generally positively correlated such that smaller hosts should contribute fewer parasites to a parasite population (eg Poulin 1999). For this reason, we offset our abundance data by host size. It is therefore important to consider that parasites may be declining, and this may possibly be unrelated to host size.

Parasites can be sensitive to environmental changes, at times to an even greater degree than their hosts. Parasite ontogeny can be perturbed by temperature changes (Morley and Lewis 2015, 2017), and pollution can reduce parasite survival and infectivity (Morley 2010). For example, development and hatching of trematode parasite eggs and trematode infectivity diminish when temperatures are above their optimal ranges (Morley and Lewis 2015, 2017). Changes in parasite abundance may therefore be directly related to their physiological responses to dynamic abiotic conditions.

Past studies have shown that abundances of complex life-cycle parasites fall in response to spatial variations in fishing pressure (eg Wood *et al.* 2015) and reductions in host species richness (eg Wood *et al.* 2018). Yet the outcome of our meta-regression suggests that transmission mode is not a predictor of temporal change in abundance; in general, our results indicate that the unique natural history of each host–parasite pair is more important than the general life history traits associated with each broad taxonomic group in determining a parasite's response to environmental change.

The specimens that are ultimately accessioned into natural history collections are not always representative of the populations from which they were sampled, and this can introduce bias into the parasitological data obtained from collections. Most holdings are biased toward smaller fish species and individuals due to collection storage capacity, which indirectly influences the number and type of parasites found. We controlled for host body size bias by selecting similarly sized fish and offsetting the response variable by host size in statistical models. However, preserved fish may also over- or underrepresent parasitized specimens, particularly if parasitic infection is visible to individuals choosing specimens for accessioning. During collection and preservation, external parasites may be dislodged or be purposefully or accidentally removed from their hosts. If our study was confounded with systematic bias due to the collection process, then one would expect that there would be either a decrease or increase in all parasites over time, and this was not the case.

Although the sampling and collection process does not affect the abundance of internal parasites detected, fluid-preservation includes a formalin fixation step, precluding our capacity for molecular identification of the parasites we counted. Accordingly, our parasite vouchers were identified and verified by multiple parasitological experts using the morphological features of each parasite and appropriate taxonomic keys (WebPanel 1). We present our data at the finest possible taxonomic resolution, which, for some taxa, was higher than genus level to remain conservative. A photographic identification guide describing each parasite taxon is publicly available via our GitHub repository.

This study is the first to use specimens from natural history collections to reconstruct a continuous time series of change in the abundance of parasites over a 90-year period. We found complex changes in English sole parasite burden over that timespan, as abundances of most parasites remained more or less unchanged over the nine decades, but declined in several and increased in one. The next step in our research will therefore be to identify the environmental variables driving the rise and fall of these parasites by pairing the historical parasite data we collected for this study with long-term datasets on fish abundance and anthropogenic change.

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