



Decapod fisheries and parasite species richness: an exploration of host traits and parasitic influence

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Abstract Some hosts harbor more parasites than others. Overdispersion of parasitism suggests that coevolution with parasites may be more important to the biology and ecology of certain species. We examined patterns of parasitism and host traits in fished decapod crustaceans, which are economically and ecologically important worldwide. Using a synthesis approach, we determine that host life history, including habitat, longevity, sociality, invasion history, and fisheries involvement, correlate with the number and type of parasite species harbored. Indicator species analysis revealed close relationships between decapods and certain parasite groups, including crabs with rhizocephalans and dinoflagellates; crayfish with mesomycetozoans, oomycetes, branchiobdellids,

and fungi; lobsters with copepods and amoebae; and shrimp with viruses. In contrast, Nematomorpha and Nemertea appear to be under-represented and under-studied as parasite groups in decapods. Decapods that are commercially fished, aquacultured, introduced outside their native range, and/or exhibit parental care tend to have higher parasite species richness (PSR). Parasite richness also increases with how well-studied a host group is, which we addressed with a machine learning algorithm that predicts false negative associations. Geographic range is commonly positively correlated with parasite richness, however reliable ranges are not available for most decapod species, highlighting a significant future research need. Identifying patterns such as these increases our broad understanding of decapod disease ecology but also enabled us to develop a series of recommendations on how to focus

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future research, management, and aquaculture development efforts.

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Introduction

Wild fisheries and aquaculture support global economies and take advantage of an abundance of protein-rich organisms, including crustaceans (Stentiford et al. 2020; Behringer and Duermit-Moreau 2021). The United Nations Food and Agriculture Organization (FAO) tracks ~200 crustacean commercial fisheries and aquaculture that produced 16.5 million metric tons in 2019 (FAO 2021), an increase from 11.7 million metric tons in 2016, which was worth over \$50 billion USD (FAO 2018). The capacity for fisheries and aquaculture to produce yield can be limited by the environment and an organism's biological or ecological requirements, but the most dramatic limits are often imposed by parasitic diseases (Stentiford et al. 2012).

Crustaceans suffer from a wide range of parasitism and disease that can increase mortality, stunt growth, limit recruitment and, ultimately, reduce yield or decrease marketability (Cawthorn 2011; Shields 2011; Lafferty et al. 2015; Bojko and Ovcharenko 2019; Arulmoorthy et al. 2020). Impacts from these parasites can cause great economic damage as well. For example, *Hematodinium perezii*, a generalist parasite, is estimated to cause losses upward of \$1 million USD per year in the US blue crab *Callinectes sapidus* fishery alone (Stentiford and Shields 2005). Aquaculture losses are easier to assess and are estimated to exceed \$6 billion USD per year across all sectors due to disease (Stentiford et al. 2017, 2020). A striking example is the impact of white spot syndrome virus (WSSV), which cost the penaeid shrimp aquaculture industry \$8–12 billion USD as of 2012 (Stentiford et al. 2012).

Most animal species host one or more parasites (Price 1980), yet parasitism is not evenly distributed among host groups or individuals (Dritschilo et al. 1975; Nunn et al. 2003; Luis et al. 2013). Some hosts harbor few parasite species, whereas others harbor a diversity of parasites and diseases. Parasites impact

behavior, growth, survival, and reproduction (Valenzuela-Sánchez et al. 2021), playing a nuanced role in the evolutionary trade-offs between survival and reproduction (Hochberg et al. 1992). For example, toad populations long exposed to the fungal disease chytridiomycosis breed at smaller sizes than before exposure, suggesting that they breed earlier (Lampo et al. 2022). Valenzuela-Sánchez et al. (2021) show similar patterns in many species of vertebrates exposed to a variety of diseases/parasites, suggesting that coevolution with parasites may be of greater importance to the biology and ecology of some groups over others.

Here, we provide the most thorough synthesis to date of decapod hosts and their parasites, using Linear Discriminant Analysis (LDA) and Indicator Species Analysis to explore correlations and distinctions between host groups, their traits, and their parasites. Our analysis seeks to increase the understanding of disease in decapods and provides information for managers and researchers on where future efforts should focus.

Life history traits of decapod crustaceans

The Food and Agriculture Organization of the United Nations (FAO) curates a list of species in capture fisheries, aquaculture, and 'of-interest' to these sectors in their global fishery production database (FAO 2017). Species 'of-interest' to the FAO are not commercially captured but may be captured in small artisanal or recreational fisheries. On the FAO list, 915 are decapod crustaceans. We subsampled from this list for decapods with a longevity estimate and at least one known parasite in wild populations ($n=101$). Life history data was compiled for each of these species on habitat, sociality, invasion history, and use in commercial fisheries or production.

Decapod hosts were grouped taxonomically as 'crab' (families: Calappidae, Cancridae, Galatheididae, Geryonidae, Grapsidae, Lithodidae, Majidae, Ocypodidae, Oregoniidae, Portunidae, Xanthidae), 'crayfish' (Astacidae, Cambaridae, Parastacidae), 'lobster' (Nephropidae, Palinuridae), or 'shrimp' (Callinassidae, Crangonidae, Palaemonidae, Pandalidae, Penaeidae, Solenoceridae, Upogebiidae) (FAO 2017). Taxonomic groups were then used in Linear Discriminant Analysis (LDA) using the MASS package in

R (Venables and Ripley 2002) on host characteristics, to determine which characteristics best differentiated the groups. While this is not the only suitable approach, LDA is specifically useful as a multivariate approach for determining which set of host characteristics are useful for discriminating between and classifying taxa into groups. Characteristics in the full model included: longevity; log of the number of parasite citations; and binary variables (0/1) for non-mutually exclusive membership to: habitat classes (euryhaline, freshwater, marine); fishery practices (aquaculture, capture, no commercial production); introduced or native; and sociality (gregarious, parental care, reproductive aggregations, solitary). Step-wise model selection using Wilks lambda from the *klaR* package (Weihs et al. 2005) was used to choose the best model, retaining only the host characteristics that significantly distinguish groups and subsequently removing collinear variables. Each host characteristic was compared between the groups using analysis of variance (ANOVA) for continuous variables and chi-square tests (with Yate's continuity correction when expected values < 5) on categorical variables (R Core Team 2021). The final LDA model for the taxonomic host groups included the following host characteristics: longevity, parental care, solitary, reproductive aggregations, marine, and non-commercial species (Fig. 1a).

Longevity

Age and lifespan are important in the management of fished species and vital for stock assessment (Campana 2001; Sheehy and Prior 2008). Accurately ageing decapod crustaceans has proved difficult historically, in part because hard structures [which are used in ageing molluscs (Schöne et al. 2005), fish (Skurdal et al. 1985), and urchins (Flores et al. 2010)] are shed during molting. Methods used to age crustaceans have varied in their reliability and include captive rearing, mark-recapture, growth models, and lipofuscin pigment analysis (Vogt 2012). More recently, researchers have been working to verify the reliability of bands deposited on the gastric mill to establish chronological age (Kilada and Driscoll 2017; Gnanalingam et al. 2019), and DNA methylation techniques have shown promise as a molecular-based method of aging a wide variety of organisms, including crustaceans (Fairfield et al. 2021). Our dataset includes longevity estimates

from peer-reviewed literature that utilizes these methods (Suppl. Table 1).

Longevity is a significant, though weak, differentiator between taxa in the LDA model (Fig. 1a). Lobsters are longer-lived than all other groups, shrimp are shorter-lived, and crab and crayfish are intermediate ($F=29.9$, $df=3,97$, $p<0.001$; Table 1; Suppl. Fig. 1a). Age estimation methods, namely captive rearing, are biased towards shorter-lived species, which is reflected in our dataset with 62.4% of the species under 5 years maximum longevity. Many species of large decapods are thought to live many decades but do not yet have reliable lifespan estimates. In our dataset, there is a 72-fold difference between the shortest-lived species, which live to one year and are all shrimp: *Palaemonetes paludosus*, *Penaeus indicus*, *Penaeus longistylus*, *Penaeus vannamei* and the longest-lived (72-year lifespan) species, the European lobster *Homarus gammarus* (Suppl. Table 1).

Longer-lived species often support lucrative fisheries, in part due to indeterminate growth and their resulting large size. The American lobster *Homarus americanus* is estimated to live upwards of 50 years and is the most valuable fishery in North America (Finch 1994; le Bris et al. 2018). However, because long-lived species also tend to mature later (5–9 years for *H. americanus*; le Bris et al. 2017) and larger individuals with greater reproductive output are sought (Koopman et al. 2015), they are more susceptible to overfishing (Beamish et al. 2006). The European and American lobster fisheries have both experienced stock declines in recent decades (Pettersen et al. 2009; Howell 2012). Longer-lived animals also tend to be difficult to rear in aquaculture, as it can take many years to reach a marketable size. In contrast, short-lived species are more commonly aquacultured, probably because their faster time to market makes them more profitable, easier to manage, and the economic losses due to disease are less catastrophic on a per outbreak basis. Whiteleg shrimp (*P. vannamei*) fit this paradigm and have become the most heavily aquacultured crustacean worldwide (FAO 2018).

Evolutionary theory predicts that parasitized individuals can increase their fitness by diverting energy toward reproduction and immunity and away from longevity (Hochberg et al. 1992). This strategy can drive a population or species towards *r*-selected life history traits, including shorter lifespan, if infection with virulent pathogens is relatively common. This

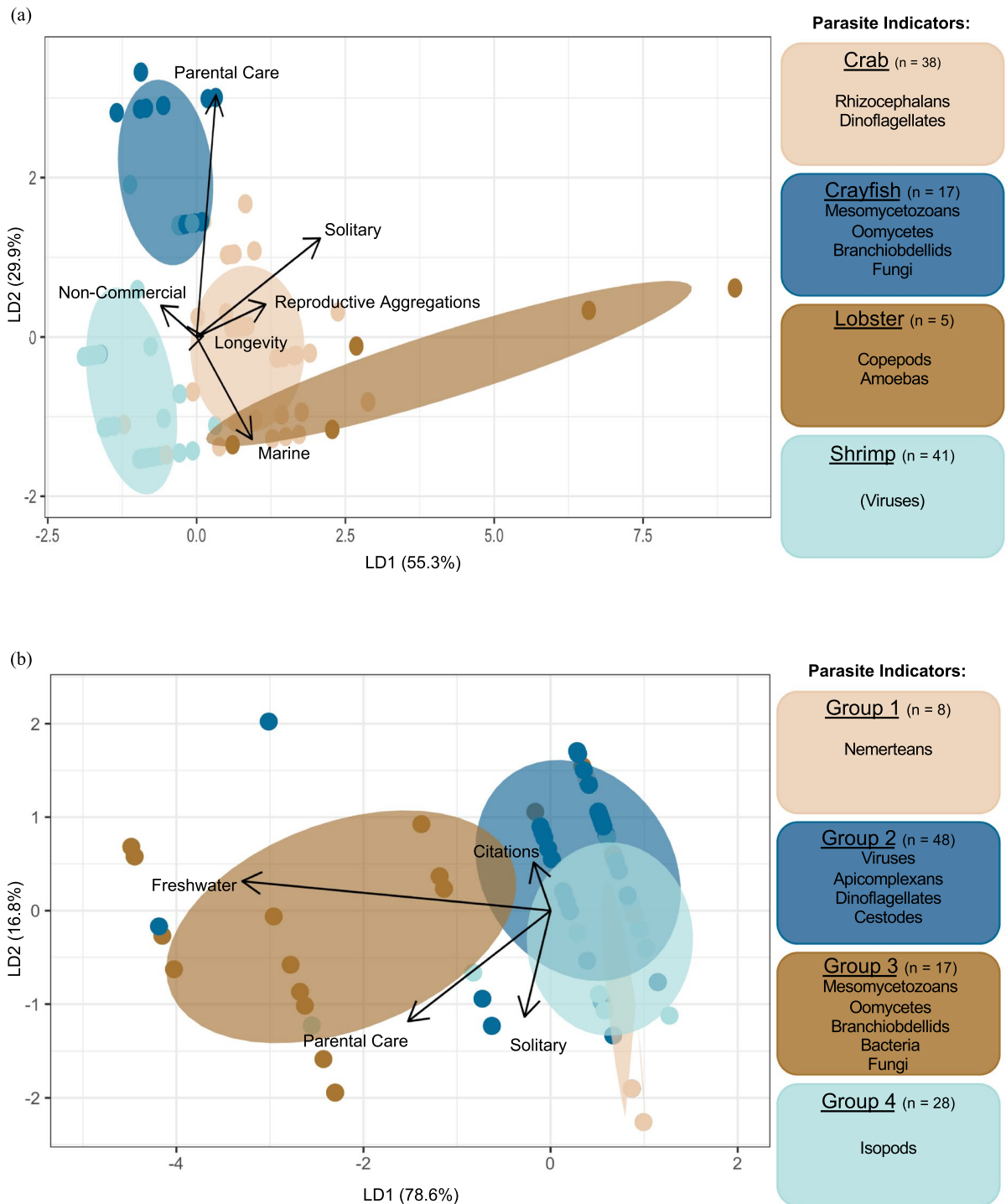


Fig. 1 Linear discriminant analysis of decapod crustacean host characteristics. **a** In taxonomic host groups and **b** in polythetic agglomerative clusters based on parasite associations. Significant parasite associations based on indicator species

analysis are given in legend on right. Arrows depict the direction and strength (i.e. length of arrow) of host life history characteristic associations

Table 1 Summary statistics for decapod crustacean taxa grouped by life history characteristic

		Crab	Crayfish	Lobster	Shrimp
Habitat	n	38	17	5	41
	FW	0	82.4	0	0
	Marine	76.3	0	100	63.4
	Euryhaline	23.7	17.6	0	36.6
Introduced	Yes	31.6	52.9	20	31.7
Sociality	Gregarious	18.4	5.9	40	82.9
	Solitary	55.3	47.1	60	4.9
	Parental care	2.6	47.1	0	4.9
	Reproductive aggregations	23.7	0	0	7.3
Fisheries	Aquaculture	21.1	35.3	20	34.1
	Capture Fisheries	65.8	35.3	100	65.9
	Longevity	8.1 ± 6.6	6.3 ± 5.0	36.4 ± 24.5	2.7 ± 2.4
	Citations	36.0 ± 66.0	45.2 ± 67.4	80.6 ± 85.0	94.5 ± 305.0

Within each categorical characteristic (habitat, introduced, sociality, and fisheries) the numbers represent the percentage of species in a particular taxon that fit a given life history characteristic. These percentages sum to 100 vertically within each category except within fisheries where species can be in both aquaculture and capture fisheries, or in neither. Longevity is given in years (mean ± sd), citations are given in number (mean ± sd), and n is the number of species in each taxon

association has been demonstrated in snails (Hochberg et al. 1992) and mammals (Morand and Harvey 2000). Alternatively, long-lived hosts may offer a more stable environment for parasitic infection (Poulin and Morand 2000).

Prediction: If evolution has driven more highly parasitized species toward *r*-selected life history traits then shorter-lived hosts will have higher PSR.

Alternative prediction: If parasites prefer a stable environment for parasitic infection, then longer-lived hosts will have higher PSR.

Habitat

Salinity tolerance is a major factor in species distribution (de Jonge 1974; Chakraborty et al. 2011) and can impact many aspects of commercial fisheries. Our analysis of FAO fishery data from 2019 indicates that most crustaceans harvested in capture and aquaculture fisheries come from brackish water (38.0%), followed by marine (34.0%), then freshwater (28.0%; FAO 2021). We categorized each species as marine, freshwater, or euryhaline based on the World Register of Marine Species (WoRMS; Horton et al. 2018; Suppl. Table 1). Species that were categorized by WoRMS as ‘brackish’ or under multiple habitats were deemed ‘euryhaline’ here. It is clear that habitat differs among the taxonomic groups ($X^2 = 86.1$, $df = 6$,

$p < 0.001$; Table 1; Fig. 2a)—e.g. All lobsters are marine, most crayfish are freshwater species, and crab and shrimp are mostly marine with some euryhaline or freshwater species (Fig. 1a).

Prediction: If euryhaline hosts are susceptible to parasites with a variety of salinity tolerances and likely to encounter different parasite species in lower versus higher salinity portions of their range, then euryhaline hosts will have greater PSR.

Sociality

Animals range from colonial/eusocial species to solitary ones, with most falling somewhere in between. Aggregation and social behaviors evolve when “the net benefits of close association with conspecifics exceed the costs” (Silk 2007). Benefits of close association include predator avoidance (Neill and Cullen 1974), reproduction (Stone et al. 1993), and parental care (Thiel 2003), while costs include parasite transmission (Arneberg et al. 1998), resource competition (Korb and Heinze 2016), and agonistic behaviors (Sinclair 1977). Social aggregations are often exploited in capture fisheries, which may select against social behavior by selectively capturing large schools (Guerra et al. 2020).

Four categories of sociality were defined and decapods were categorized based on peer-reviewed

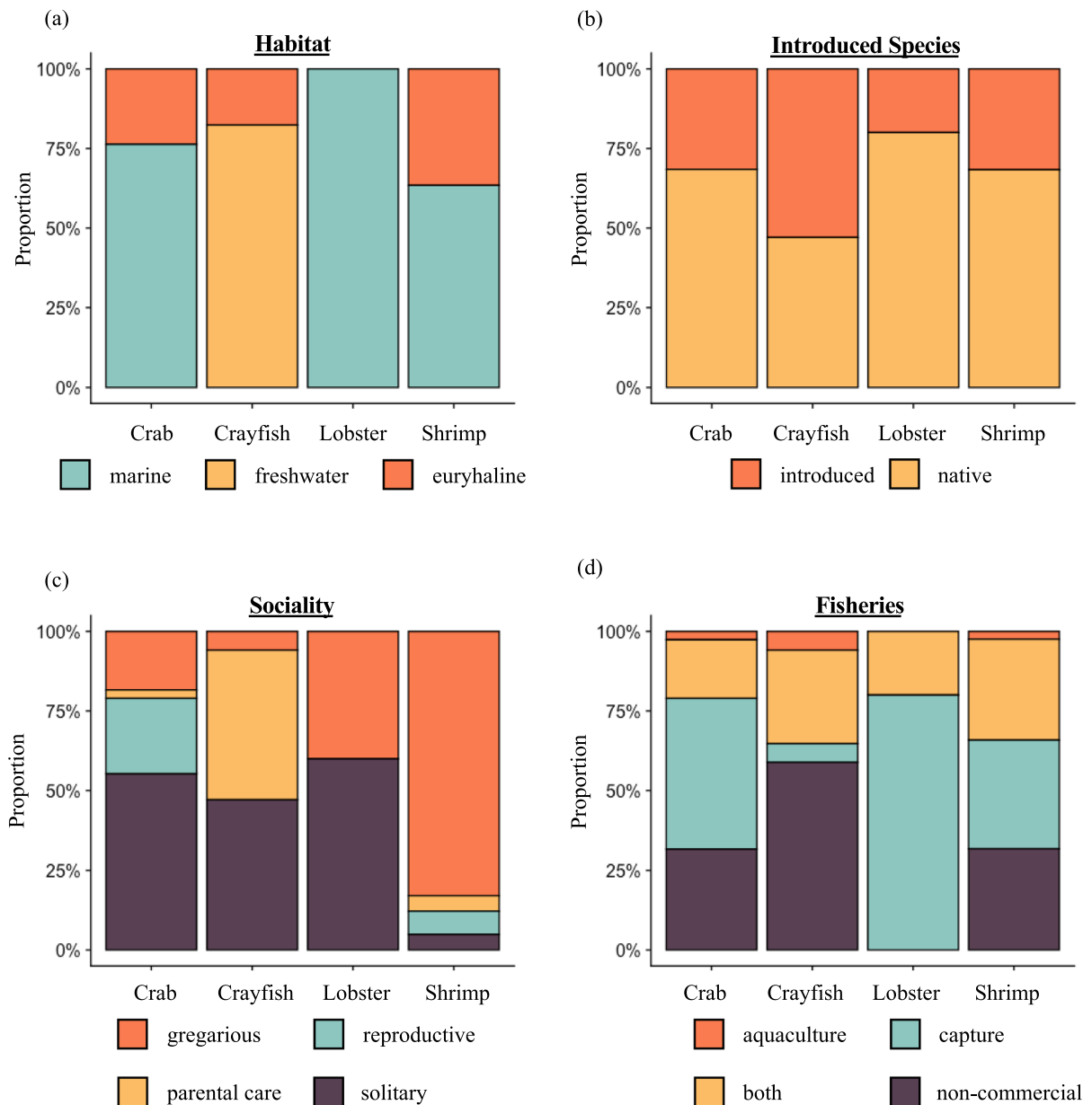


Fig. 2 Stacked bar charts showing the breakdown of host characteristics by taxonomic groups. Host characteristics are **a** habitat, **b** introduced species, **c** sociality, and **d** fisheries exploitation

literature (Suppl. Table 1). Categories are as follows: (1) ‘gregarious’ species are those known to regularly aggregate; (2) ‘solitary’ species generally reside alone, encountering conspecifics for mating in pairs, not in large groups; (3) species with ‘reproductive aggregations’ form large pods for molting, mating, and/or spawning; and (4) species with ‘parental care’

have aggregations of juveniles with parents (typically the female parent) during early life stages, but other stages are solitary.

Sociality was a strong differentiator in the taxonomic LDA (Fig. 1a), significantly differentiating the taxa ($X^2=75.4$, $df=9$, $p<0.001$; Table 1; Fig. 2c). Shrimp are comprised of species with all sociality

types but are largely gregarious. A gregarious nature benefits commercial fisheries using seines and trawls to capture large schools (Tulian 1920; Xiao and Greenwood 1993) and benefits aquaculture in allowing for high stocking densities (Bardera et al. 2019). Lobsters can be solitary or gregarious, often depending on whether they are clawed or spiny, respectively. Gregariousness in the Caribbean spiny lobster, *Panulirus argus*, is used to the advantage of the fishery. In Florida, traps are baited with live juvenile lobsters that attract legal lobsters using chemosensory cues (Hunt et al. 1986), and elsewhere, lobsters aggregate in casitas for divers to capture. Like clawed lobsters, crabs are largely solitary. The Florida stone crab, *Menippe mercenaria*, is prized for its large claws, which are the only landed product (Gandy et al. 2016; Duermit et al. 2017). They live a largely solitary life, using these claws in agonistic encounters with conspecifics (Sinclair 1977), only cohabitating for reproduction and mate-guarding (Wilber 1989). Crabs also have the largest proportion of reproductive aggregations, often referred to as “podding” behavior. These pods protect individuals during the vulnerable molting period and subsequent mating (Carlisle 1954). Pods have been utilized by fishers for centuries (Štević 1971) and Stone et al. (1993) hypothesized that their existence in the economically valuable red king crab, *Paralithodes camtschaticus*, may have led to overexploitation, resulting in fishery collapse and closure in 1983. Crayfish exhibit more parental care than other decapods. Many decapods incubate eggs on the underside of their abdomen until hatching, but crayfish juveniles often remain with their mother and siblings for weeks to months for further protection, potentially as an adaptation to higher current and different dispersal needs in freshwater habitats (Scholtz and Kawai 2002). Efforts to exploit this trait to increase aquaculture production have not been fruitful (Patoka et al. 2013).

Prediction: If greater interaction among conspecifics increase opportunity for direct transmission of parasites (Anderson and May 1982) then gregarious hosts will have higher PSR than hosts with other social systems.

Introduced species

Invasive and non-native species (INNS) can present great risks to native fauna (Wilcove et al. 1998) and

economies (Pimentel et al. 2005; Cook et al. 2007). While most introductions are accidental, they tend to be associated with anthropogenic sources, including fishing and aquaculture. The red claw crayfish, *Cherax quadricarinatus*, has been introduced to many regions due to its high value in aquaculture. In Mexico, poor management of aquaculture ponds led to the escape and establishment of this species, which is now a significant portion of the catch in the native *Macrobrachium americanum* fishery (Vega-Villasante et al. 2015). Fishing can also be used as a method of control for invasive species, e.g., blue crab *Callinectes sapidus*, native to the western hemisphere, invasive and fished in the Mediterranean (Mancinelli et al. 2017).

Using the Global Invasive Species Database Information System on Aquatic Non-Indigenous and Cryptogenic Species, and the European Alien Species Information Network (EASIN) [following methods in (Bojko et al. 2021)] we categorized our decapods as species that have been introduced or species that have not been introduced (Suppl. Table 1). For simplicity, these will be referred to as “introduced” and “native”, respectively, though parasites of introduced hosts are also included from the native ranges. Overall, 34.7% of species in the dataset are introduced and the proportion of introduced species did not differ by taxonomic group ($X^2 = 3.3$, $df = 3$, $p = 0.35$; Table 1; Fig. 2b). Introduction was not a significant indicator in the taxonomic LDA (Fig. 1a).

There are two major hypotheses for the diversity of parasites in introduced species. First, the “parasite acquisition hypothesis” sometimes referred to as “parasite spillover and spillback” (Kelly et al. 2009) claims that introduced species have greater parasite diversity, because they can acquire parasites in both their native and introduced ranges and these ranges are likely to have different parasites. The second is an extension of the “enemy release hypothesis” (Colautti et al. 2004), which suggests that a species with many parasites (enemies) in its native range is likely to be introduced without those parasites, allowing for its proliferation and success in the invasive range. This hypothesis suggests that species with many enemies in their native range are more likely to become invasive because of this release. These hypotheses are not mutually exclusive and have been documented to act simultaneously (Sheath et al. 2015).

Prediction: If parasite acquisition and/or enemy release occur then hosts that are introduced will have greater PSR, when accounting for both their native and introduced ranges, than hosts living in their native range only (native).

Aquaculture and commercial fisheries

We categorized species as a part of aquaculture, commercial capture fisheries, both, or neither (“non-commercial”; Suppl. Table 1). Species designated by the FAO as non-commercial are not currently exploited commercially but they are of interest to the FAO, indicating that there may be small artisanal or recreational fisheries, or fisheries and aquaculture are being explored. Overall, 25.7% of species are both cultured and fished: 3.0% in aquaculture only, and 36.6% capture only. We included aquacultured species, but we excluded parasites found only in aquaculture settings, since their wildlife origin or natural evolution is difficult to untangle in parasitological literature.

“Non-commercial” was a moderate differentiator between groups in the taxonomic LDA (Fig. 1a). The crab and lobster taxa are negatively associated with “non-commercial” (i.e. they are commercially exploited). All lobster species in our dataset are exploited in capture fisheries or in both capture and aquaculture. In our dataset, 34.2% of crabs are not exploited in capture or aquaculture.

Prediction: If aquaculture provides many routes for release and introduction of pathogens to wild populations, such as introduction of infected stocks, movement of equipment and fish products, viral and bacterial evolution, and exposure to environmental reservoirs (Murray and Peeler 2005), then wild hosts that are also in aquaculture will have greater PSR.

Alternative prediction: If aquacultured and captured hosts are examined more thoroughly due to their fisheries interest, then these hosts will have greater PSR.

Species sampling intensity

Sampling intensity varies widely between species and, in general, the more a species is studied, the more parasites tend to be found (Poulin 1997). We accounted for sampling intensity via the number of citations on Web of Science for the species name (and common synonyms/previous names) ‘AND

pathogen* OR parasite* OR disease*’ in the title or abstract (Suppl. Table 1). In this dataset, 37.6% of species have five or fewer citations mentioning parasite keywords, but two species have >500: *P. vannamei* (1,717) and *P. monodon* (940). These extreme numbers likely reflect that these are the two top aquacultured species worldwide (Thitamadee et al. 2016). Despite this gap, the taxonomic groups are not significantly different in how well-studied they are regarding parasitism ($F=0.77$, $df=3,97$, $p=0.51$; Table 1; Fig. 3a). Sampling intensity was not an important factor in the taxonomic LDA (Fig. 1a).

We examined additional models that accounted for total species sampling intensity (i.e. not necessarily related to disease research). These variables were

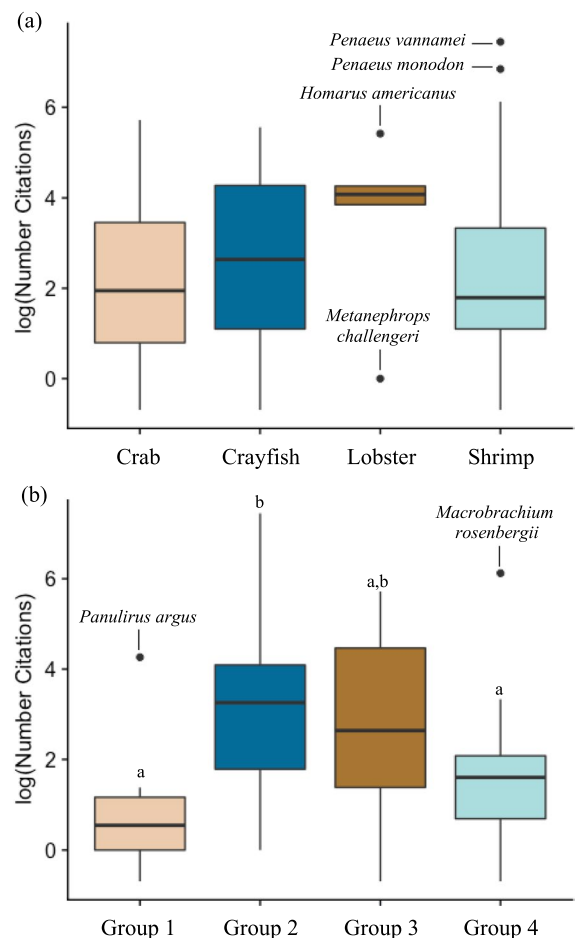


Fig. 3 The log of number of parasite citations for **a** taxonomic host groups and **b** host groups created by polythetic agglomerative clustering based on parasite assemblages. Lowercase letters above boxes indicate significant differences

highly correlated (0.90) and in this case (and all cases hereafter) these models were nearly identical to those that use pathogen search results instead. We chose to include pathogen search results because LDA models that included this term explained slightly more variance than those that included total host species search results.

False negative estimation

Despite the lack of relationship between sampling intensity and the taxonomic groups, there is a positive relationship between sampling intensity and reported PSR ($R^2=0.35$; see Supplemental Materials). This pattern suggests that we may be missing many possible parasite-host relationships because they have not been studied, resulting in false negatives in our dataset. To model the probability of given unobserved linkage being a false negative, we predicted the probability of a linkage

occurring between a given parasite species infecting one host species using Ensemble Random Forests (ERF; Siders et al. 2020), a machine learning algorithm designed to model rare event data (see detailed methods and results in Supplemental Material). Using the linkages sampled in the literature review, the probability of all parasite-host linkages was predicted assuming the maximum sampling intensity and then the probability of a given linkage being a false negative was calculated using the (Morton et al. 2021) approach. Across the 48 ‘host type’ and ‘pathogen group’ interactions, 11 increased the odds of a parasite-host linkage by more than 50% indicating a high chance of linkages occurring between these host types and pathogen groups (Fig. 4). These false negatives were not further included in analyses but are used as discussion points below to identify and examine areas where under sampling could lead to biases.

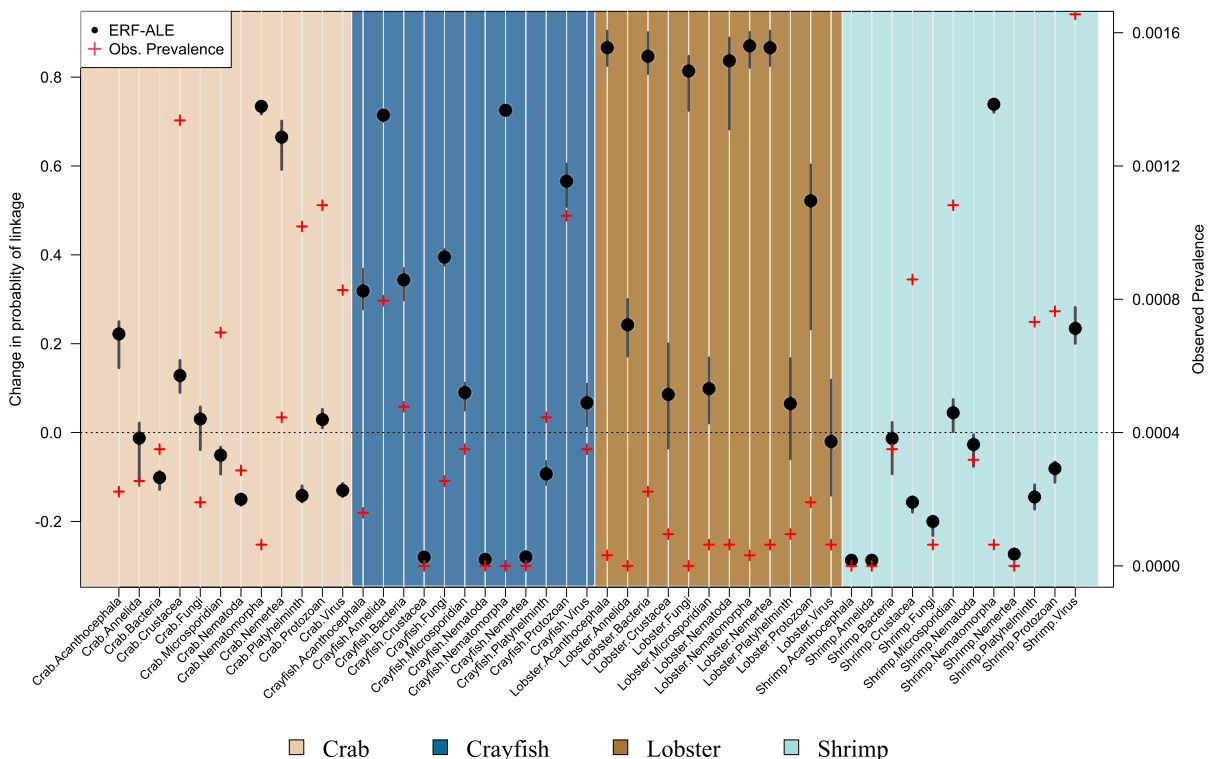


Fig. 4 Accumulated local effects of the host type and pathogen group interactions measuring the change in the ensemble random forests predicted linkage probability with the circle indicating the median value and the segment indicating the

90% confidence interval. Also shown is the observed prevalence of host type and pathogen group links from the 31,412 possible links

Parasite species richness in fished decapods

Parasites and their characteristics were compiled by searching Web of Science and Google Scholar for each decapod species of interest ‘AND pathogen* OR parasite* OR virus’ (year-range: 1864–2020). Commensal symbionts were excluded, as were parasites that were not identified to the genus level (excluding viruses, which were identified to the family level). Parasites were classified by their higher taxonomy (Acanthocephala, Amoebae, Apicomplexa, Bacteria, Branchiobdellida, Cestoda, Ciliophora, Copepoda, Dinoflagellate, Fungi, Haplosporidia, Isopoda, Hirudinea, Mesomycetozoa, Microsporidia, Nematoda, Nematomorpha, Nemertea, Oomycete, Paramixida, Rhizocephala, Trematoda, or Virus). Relationships between parasite and host were categorized as natural (i.e. detected in wild populations), cultured (i.e. only seen in aquaculture setting), or both natural and cultured. For this analysis, passaged parasites (i.e. pathogenicity only known from laboratory inoculation) and those found exclusively in aquaculture were excluded from the dataset. Decapods host 311 known parasites and a total of 550 parasite-host associations have been recorded (Fig. 5a). The groups accounting for the most parasite-host relationships are protozoans (Amoeba, Apicomplexa, Ciliophora, Dinoflagellate, Haplosporidia, Mesomycetozoa, Oomycete,

Paramixida) (18%) and viruses (*Birnaviridae*, *Bunyavirales*, *Cruliviridae*, *Dicistroviridae*, *Mininucleoviridae*, *Nidovirales*, *Nimaviridae*, *Nodaviridae*, *Nudiviridae*, *Parvoviridae*, *Picornaviridae*, *Reoviridae*, *Rhabdoviridae*, *Tombusviridae*, *Totiviridae*) (17%). Variation in the number of parasites per host species (PSR) was analyzed using generalized linear mixed effect models (GLMM) with a negative binomial fit for count data in the package *glmmTMB* (Brooks et al. 2017). Differences between groups were then analyzed with Analysis of Variance using the *car* package (Fox 2011).

Taxonomic host groups have distinct parasite assemblages (PERMANOVA: $F=6.3$, $R^2=0.16$, $p<0.001$; Fig. 5b), except crab and lobster ($F=1.2$, $R^2=0.03$, $p=0.31$). Indicator species analysis, which combines a parasite’s host fidelity and relative abundance and predicts the probability of finding a higher indicator value in another taxon (Dufrene and Legendre 1997), revealed eight parasite taxa strongly associated with host taxa (Fig. 1a). Rhizocephalans and dinoflagellates were indicators of the crab group (indicator value = $d=0.33$, $p=0.03$ and $d=0.29$, $p=0.04$, respectively); the crayfish group was indicated by mesomycetozoans ($d=0.76$, $p=0.001$), oomycetes ($d=0.51$, $p=0.003$), branchiobdellids ($d=0.51$, $p=0.001$) and fungi ($d=0.25$, $p=0.03$); and indicators of the lobsters were copepods

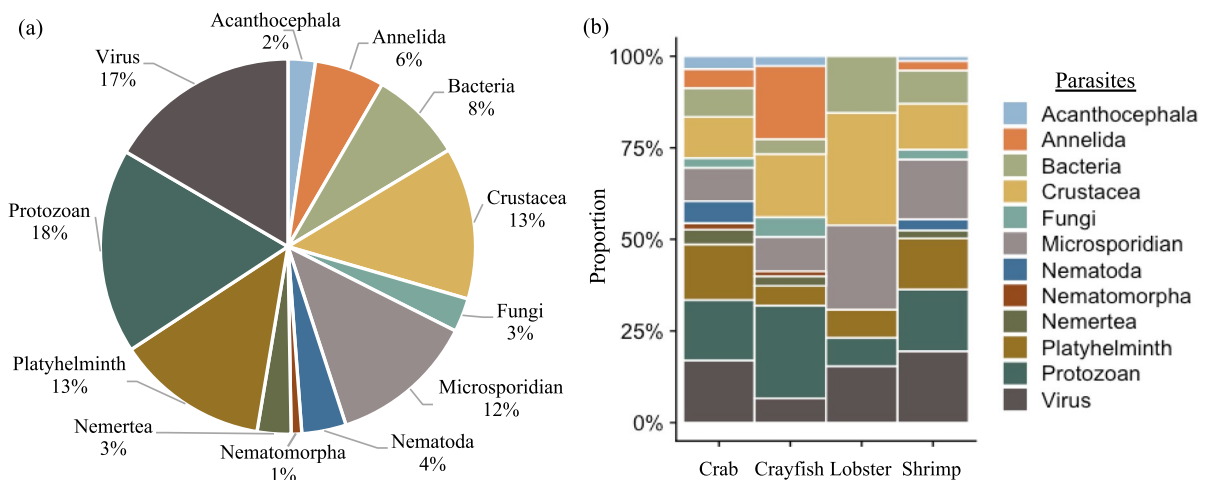


Fig. 5 The relative number of parasite taxonomic groups in wild populations of decapod crustaceans: **a** all groups combined and **b** by host group. Several taxa are grouped here that are kept separate for analyses: Annelida (Brachiobdella, Hir-

udinea), Crustacea (Rhizocephala, Isopoda), Platyhelminth (Cestoda, Trematoda), and Protozoan (Amoeba, Apicomplexa, Ciliophora, Dinoflagellate, Haplosporidia, Mesomycetozoa, Oomycete, Paramixida)

($d=0.33$, $p=0.01$) and amoebae ($d=0.18$, $p=0.04$). There were no statistically significant parasite indicators for shrimp (but see Sect. “[Shrimp parasites](#)”). Overall, crayfish had a significantly greater reported PSR than shrimp (Fig. 6a; $F=10.6$, $df=3$, $p=0.014$) but other pairwise differences were not significant.

Crab parasites

Rhizocephalans are parasitic barnacles that can infect decapods, molluscs, or can be free-living (Høeg 1995; Boyko and Williams 2009). In our dataset they are exclusive to crabs (Anomura and Brachyura), with brachyurans accounting for two-thirds of all known hosts (Shields et al. 2015). Female rhizocephalans infect their host with an endoparasitic internal

phase before extruding a virgin externa through the host’s abdomen, which attracts males for reproduction (Høeg 1995). These parasites castrate male and female crabs (O’Brien and Wan Wyk 1985) often altering host behavior (Toscano et al. 2014). Rhizocephalans affect crab marketability and recruitment, often causing issues for fisheries (Lafferty et al. 2015).

Dinoflagellate parasites are represented by *Hematodinium* spp. in our dataset, though this is not the only dinoflagellate parasite of crustaceans (Stentiford and Shields 2005). These parasites appear to be generalists among brachyurans but can also infect wild Norway lobster *Nephrops norvegicus* (Field and Appleton 1995), cultured ridgetail prawn *Exopalaemon carinicauda* (Xu et al. 2010) and giant tiger prawn *P. monodon* (Wang et al. 2017), and amphipods (Messick and Shields 2000). *Hematodinium* sp. proliferates in the hemolymph, leading to a milky appearance, which is often accompanied by hyperpigmentation of the exoskeleton, similar to a cooked animal (Small 2012). Other clinical signs have led to a range of syndromes, notably Bitter Crab Disease (BCD) in important capture fisheries including snow and tanner crabs *Chionoecetes* spp., the velvet crab *Necora puber*, and the king crabs *Paralithodes camtschaticus* and *P. platypus* (Meyers et al. 1987; Wilhelm and Mialhe 1996; Ryazanova 2008). Infection can also proliferate in aquaculture systems and transmit between susceptible species in polyculture systems (Xu et al. 2010; Wang et al. 2017). Economic impacts from this parasite are difficult to calculate but have ranged from \$250,000 USD to nearly \$10 million USD for various fisheries (Stentiford and Shields 2005).

From the ERF, we estimated that there are two groups of crab parasites that are underrepresented in our dataset: Nematomorpha and Nemertea. Nemer-teans are quite prevalent as egg predators and gill parasites in crabs and lobsters but are understudied despite the potential for massive brood mortality and associated population and evolutionary consequences (Kuris and Wickham 1987). Wickham (1979) estimated that epidemic levels of the nemertean *Carcinonemertes errans* on the Dungeness crab *Cancer magister* was causing direct mortality of 55% of eggs produced and could lead to local fishery collapse.

Nematomorpha are seemingly a much rarer, though underreported, parasite of decapods, with

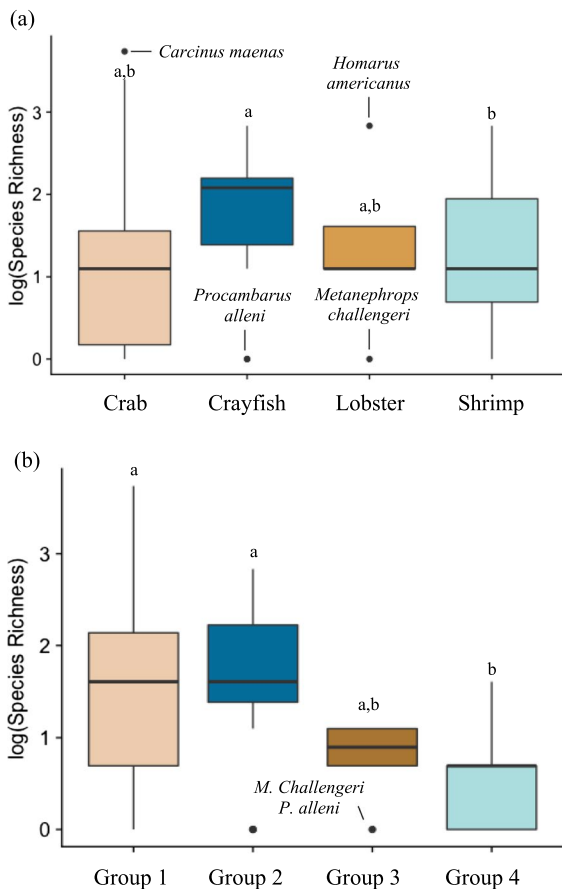


Fig. 6 Species richness for **a** taxonomic host groups and **b** host groups created by polythetic agglomerative clustering based on parasite assemblages. Lowercase letters above boxes indicate significant differences

only five instances in our dataset, two of which are in crab hosts. They are represented by a single genus *Nectonema*, a marine horsehair worm also infecting shrimp, lobsters, and isopods (Schmidt-Rhaesa et al. 2013; Kakui et al. 2021). Effects of these parasites on host behavior and physiology are unclear, some studies report reduced gonad size and fecundity, particularly in freshwater Nematomorpha, (summarized in Stevens 2022) though this parasite group is not well-studied.

Crayfish parasites

Branchiobdellids are obligate symbionts of crayfish and can be commensal (Longshaw 2011), mutualistic (Brown et al. 2002), or parasitic (Hobbs Jr et al. 1967). This group can elicit a host immune response in particularly heavy infestations (Alderman and Polglase 1988), have been implicated in mortality (Hubault 1935), and can transfer to sympatric crab species (Gelder et al. 2001). As obligate symbionts of crayfish, it seems likely that these groups experience some degree of coevolution; however, branchiobdellid taxonomy remains in flux (Skelton et al. 2013). While a linkage between crayfish and Branchiobdellids was common, as Annelids, this group also represents a linkage with a high change in probability from the ERF, thus there are likely false negative associations that are missed in our dataset. These false negatives may be due to branchiobdellids' common classification as crayfish commensals, which were removed from our analysis.

Mesomycetozoeans are represented by the *Psorospermium* genus (Order Ichthyophonida) in our dataset and are only noted as parasites of crayfish. This genus infects wild and aquacultured crayfish, causing significant mortalities (Cerenius et al. 1991). Mesomycetozoans are a relatively new taxonomic designation (Glockling et al. 2013) and their relationship with non-crayfish decapods as commensals versus parasites is unclear (McDermott 2011).

Fungi are a more concerning parasite of decapods, particularly the genus *Fusarium*, which causes black gill disease (Souheil et al. 1999; Mahmoud 2019). Proliferation of this filamentous fungus in the gills leads to melanization, impacting osmoregulatory ability and causing mortality that can have grave economic impacts to fisheries and aquaculture (Souheil et al. 1999). Another concerning fungal parasite is

Batrachochytrium dendrobatidis, which is implicated in the worldwide decline of amphibian species (Cheng et al. 2011). Crayfish are also susceptible to this “chytrid fungus” and may even be a reservoir and vector of the disease to amphibians (McMahon et al. 2013).

Aphanomyces astaci (oomycete; crayfish plague) has devastated crayfish in Europe, where it was introduced by invasive North American crayfish in the nineteenth century (Alderman 1996) and has since become one of the best-studied invertebrate parasites (Svoboda et al. 2017). Whereas infected European crayfish experience rapid mortality, North American crayfish are generally latent carriers of the disease suggesting that it evolved with crayfish there (Svoboda et al. 2017). Despite devastating impacts, North American crayfish are still being introduced to Europe for aquaculture purposes (Svoboda et al. 2017).

Aside from Annelids, represented largely by Branchiobdellids, the other largely underreported parasite group in crayfish, according to the ERF, is Nematomorpha. This is an intriguing correlation because there are no linkages in our dataset and we were not able to find any reports in the literature for Nematomorpha parasitizing crayfish, though crayfish predation on these worms has been documented (Cochran et al. 1999). Nematomorpha are divided into two groups—the gordiids or “freshwater horsehair worms” that infect millipeds and insects and the nectonematids or “marine horsehair worms” that infect decapods and a few other crustacean groups (Bolek et al. 2015). Thus, there may be a disconnect between host-parasite evolution and environmental needs that limits the ability of nematomorphs to parasitize freshwater crayfish, which would highlight a weakness in our false negative analysis.

Lobster parasites

Crabs and lobsters were not distinct in their parasite assemblages (Fig. 1a), though parasitic copepods and amoeba were indicators of lobsters because of their relative prevalence (40%). Parasitic copepods (*Choniosphaera* sp. and *Nicothoe astaci*) were identified in crabs and lobsters, respectively, in our dataset. In crabs, these copepods are egg predators and considered parasitic, because they live within the clutch and mimic the appearance of eggs (Gotto 2004).

Choniosphaera sp. can have a significant impact on fecundity, suggesting negative impacts to fishery recruitment, if sufficient prevalence and burden is reached (Shields and Wood 1993). In lobsters, *N. astaci* is a gill parasite that feeds on host hemolymph, can have high burden and up to 100% prevalence in populations (Wootton et al. 2011), and impedes host respiratory function (Davies et al. 2015). Impacts of *N. astaci* on lobster fisheries are not well understood, but there is evidence that adverse effects increase with stress (Gibson 1961; ICES 2007).

Consequences of amoebic infections in crustacean fisheries are better documented. *Neoparamoeba* sp. infect crab and lobster haemal spaces and connective tissue, circulating through the hemolymph in terminal infections causing tissue damage and lethargy (Johnson 1977) and infect invasive, co-habiting, *Carcinus maenas* (Bojko et al. 2018). Infection can spread rapidly in blue crab *Callinectes sapidus* shedding facilities (Shields 2012) and is implicated in the mass mortality of American lobster *H. americanus* in Long Island Sound in 1999–2000 (Mullen et al. 2004). This epidemic played a role in a local fishery collapse, where *H. americanus* catch was reduced by 90–99% (Mullen et al. 2004; Shields 2012).

Lobsters have more parasite groups with high probability of false negative than the other host taxa, possibly due to relatively low observed prevalence of parasite groups (Fig. 4). The parasite groups likely underrepresented in our dataset include Acanthocephala, Bacteria, Fungi, Nematoda, Nematomorpha, and Nemertea.

Shrimp parasites

Shrimp account for 40.6% of hosts in our dataset and 33.6% of decapod host-parasite associations. This is low given the general perception that shrimp harbor many parasites relative to other crustaceans. Lafferty et al. (2015) showed that 61.5% of crustacean diseases of economic consequence impact shrimp. However, aquaculture is the source of much of the economic losses and our dataset only included parasites that have been found in wild decapod populations. It is believed that most aquaculture parasites are sourced from wild stocks (McVicar 1997; Kurath and Winton 2011), that they impact stressed animals in crowded monoculture ponds (Kent 2000), and that most of these diseases are subsequently exported from farms

to wild populations (Lafferty et al. 2015). Infectious hypodermal and hematopoietic virus (IHHNV) is an important example of disease spillover from aquaculture to wild shrimp populations (Lightner et al. 1992). IHHNV was introduced to the Gulf of California in 1987 via a shipment of infected *P. vannamei* and spread through regional farms of *Penaeus stylirostris* (Lightner et al. 1992). By 1990, IHHNV was found in wild fisheries of *P. stylirostris*, which had declined by 50% and remained dampened for a decade (Morales-Covarrubias et al. 1999).

For these reasons, many of the viruses that cause issues in aquaculture (e.g. white spot syndrome virus, yellow-head virus, Taura syndrome virus, IHHNV) have been included in our data, and shrimp are shown to account for 57.1% of the host-virus relationships. Viruses were strong indicators of the shrimp taxon ($d=0.24$); however, this was not significant in our model ($p=0.20$), because viruses were also important, though weak, indicators of the other taxa (crab $d=0.07$, crayfish $d=0.08$, lobster $d=0.05$).

For shrimp, the parasite group most likely to be underrepresented is the Nematomorpha, discussed in more detail in Sects. “Crab parasites” and “Crayfish parasites”.

Parasite species richness and host traits

To examine how host traits influence PSR, we first grouped hosts using polythetic agglomerative hierarchical clustering (Sneath and Sokal 1973) according to a Bray–Curtis distance matrix of parasite associations (hereafter ‘agglomerative clustering’). This method is blind to host characteristics allowing us to later examine how parasite species and host characteristics are correlated. The distance matrix was calculated on parasite counts within each host species, where parasites were grouped taxonomically. The clustering method yielded four host groups with distinct parasite assemblages (PERMANOVA: $F=16.6$, $R^2=0.34$, $p<0.001$; Fig. 1b) and $n=8, 48, 17$, and 28 host species, respectively. These groups were not equivalent to the four taxonomic host groups.

Eleven parasite taxa were associated with the groups as indicator species: nemertean were indicators of Group 1 ($d=0.86$, $p=0.001$); viruses ($d=0.52$, $p=0.002$), apicomplexans ($d=0.31$, $p=0.008$), dinoflagellates ($d=0.20$, $p=0.007$), and

cestodes ($d=0.25$, $p=0.02$) were indicators of Group 2; mesomycetozoans ($d=0.76$, $p=0.001$), oomycetes ($d=0.59$, $p=0.001$), branchiobdellids ($d=0.52$, $p=0.001$), bacteria ($d=0.37$, $p=0.006$), and fungi ($d=0.25$, $p=0.015$) were indicators of Group 3; and isopods ($d=0.57$, $p=0.001$) were indicators of Group 4. Groups 1 and 2 had significantly greater PSR (Fig. 6b; $F=21.0$, $df=3$, $p<0.001$) relative to Group 4.

Host clusters were then analyzed with an LDA using host characteristics to determine which characteristics best differentiated the groups. Characteristics in the full model included longevity, log of number of parasite citations, and “dummy” variables (0/1) for habitat, fishery, introduced/native, and sociality. Step-wise model selection using Wilks lambda was used to choose the best model, retaining only the host characteristics that significantly distinguished the clusters and removing collinear variables. The final LDA model for the host clusters included the following host characteristics: freshwater, parental care, solitary, and log of number of pathogen-related citations (Fig. 1b; Table 2).

Parasites relative to host longevity

Longevity was not a strong predictor of parasite assemblages in taxonomic or agglomerative clustering groups (Fig. 1). Despite lobsters being longer-lived, shrimp shorter-lived, and crabs and crayfish intermediate (Suppl. Fig. 1a), the taxonomic LDA showed that longevity is a weak differentiator of parasite assemblage in these taxa (Fig. 1a). This result is reinforced in the agglomerative cluster LDA, where longevity was not included in the final model and did not differ among the groups ($F=0.74$, $df=3,97$, $p=0.53$; Suppl. Fig. 1b). Additionally, the association was random between longevity and reported PSR ($R^2=-0.007$, $F=0.27$, $df=1,99$, $p=0.60$). This result does not support our prediction that shorter-lived hosts will have higher PSR, which could be due to interactive effects of parasitized hosts evolving r -selected life history traits and parasites finding more stable environments in long-lived hosts. Our result may also be due to the bias towards shorter-lived species in our dataset and the overall difficulty in aging crustaceans.

Table 2 Summary statistics for decapod crustaceans polythetic agglomerative clustering and grouped by life history characteristic

		Group 1	Group 2	Group 3	Group 4
Habitat	n	8	48	17	28
	FW	0	14.3	78.6	7.1
	Marine	75	68.8	5.9	71.4
	Euryhaline	25	27.1	29.4	25
Introduced	Yes	25	39.6	58.8	14.3
Sociality	Gregarious	12.5	50	11.8	60.7
	Solitary	75	27.1	47.1	25
	Parental care	0	6.3	41.2	3.6
	Reproductive aggregations	12.5	16.7	0	10.7
Taxon	Crab	87.5	37.5	5.9	42.9
	Crayfish	0	4.2	82.3	3.6
	Lobster	12.5	6.3	0	3.6
	Shrimp	0	52.1	11.7	50
	Fisheries	Aquaculture	12.5	39.6	35.3
	Capture Fisheries	25	79.2	47.1	39.3
	Longevity	9.5 ± 11.2	7.3 ± 12.6	6.6 ± 5.0	6.1 ± 5.9
	Citations	10.6 ± 24.5	97.0 ± 277.0	60.9 ± 90.2	22.8 ± 85.2

Clustering was done according to parasite assemblages within species. Within each categorical characteristic (habitat, introduced, sociality, taxon, and fisheries) the numbers represent the percentage of species in a particular agglomerative cluster group that fit a given life history characteristic. These percentages sum to 100 vertically within each category except within fisheries where species can be in both aquaculture and capture fisheries, or neither. Longevity is given in years (mean ± sd), citations are given in number (mean ± sd), and n is the number of species in each taxon

Parasites and host habitat

In the taxonomic LDA there was a positive association between the marine habitat and lobster hosts, indicated by both copepod and amoebae parasites; and crab hosts, indicated by rhizocephalans and dinoflagellates (Fig. 1a). These results indicate that copepods, amoebae, rhizocephalans, and dinoflagellates are more likely to be found in marine hosts than elsewhere. Prevalence of rhizocephalan infections vary with salinity in estuarine crabs (Blakeslee et al. 2021) and larvae are unable to survive at low salinities (Reisser and Forward 1991). The dinoflagellate *Hematodinium* sp. is also found to infect hosts more commonly at higher salinities and, while it can survive within hosts at low salinity, cannot proliferate and transfer between hosts (Messick and Shields 2000; Coffey et al. 2012). Logically, there was a negative association between the marine habitat and crayfish hosts, which were indicated by mesomycetozoans, oomycetes, branchiobdellids, and fungi (Fig. 1a), meaning these parasite groups are less likely to be found in marine habitats. This result was supported by the agglomerative clustering LDA (Fig. 1b; Fig. 7a) where there was a strong positive association between freshwater habitats and Group 3, which was indicated by mesomycetozoans, oomycetes, branchiobdellids, bacteria, and fungi, and a negative association between freshwater and Group 4, which was indicated by parasitic isopods (Fig. 1b), which are rarer in freshwater environments. Branchiobdellids, in particular, have only been observed in freshwater environments and from freshwater hosts (Govedich et al. 2010).

There was no significant difference in reported PSR by host habitat ($F=3.1$, $df=2$, $p=0.21$; Fig. 8a), despite our prediction that euryhaline hosts would have the highest parasite species diversity because they may encounter parasite species with a variety of salinity tolerances. The blue crab *C. sapidus* provides an excellent case study as a euryhaline host with high PSR, since it is a highly efficient osmoregulator, allowing it to move freely between freshwater and saltwater, most notably during mating and spawning. Many *C. sapidus* parasites seem to be infectious in only high or low salinity water (Tindle et al. 2004; Coffey et al. 2012). Avoidance behavior may have acted as a selection pressure for the blue crab's catadromous migrations (Behringer et al. 2018). *Callinectes*

sapidus also provides an example for greater PSR in marine hosts because more parasitic species have been described in marine versus freshwater blue crabs (Shields and Overstreet 2007; Walters et al. 2023). If parasite diversity increases with geographic range, the vastness of the ocean would suggest that there should be higher parasite diversity in marine hosts. However, in fish, freshwater hosts have greater PSR than their marine counterparts (Poulin 2016). Greater diversification of species in freshwater may be due to greater habitat heterogeneity or isolation in freshwater (e.g., lakes) that leads to parasite or host speciation (Wiens 2015).

Parasites and host sociality

In the taxonomic LDA (Fig. 1a) there was a strong positive association between parental care and crayfish, which were indicated by mesomycetozoans, oomycetes, branchiobdellids, and fungi; suggesting that these parasite groups are more commonly found in hosts exhibiting parental care, with parasites possibly benefitting from vertical transmission. Crabs were associated with solitary lifestyles and are indicated by rhizocephalan barnacles and dinoflagellates. These parasite groups have complex lifecycles with free-living stages. The infectious stage is not passed directly between hosts of the same species and may not benefit from their host's social behaviors. There was a negative association between shrimp and solitary lifestyle and reproductive aggregations, meaning shrimp do not commonly have these social structures. Shrimp are pseudo-indicated by viruses (see Sect. "Shrimp parasites"), which typically do not survive well outside of a host and therefore benefit from high densities of gregarious hosts for direct transmission.

The agglomerative clustering LDA (Fig. 1b; Fig. 7c) revealed a positive association between parental care and Group 3, indicated by mesomycetozoans, oomycetes, branchiobdellids, bacteria, and fungi, reinforcing the crayfish associations in the taxonomic LDA. There were negative associations between solitary lifestyle and Group 2, indicated by viruses, apicomplexans, dinoflagellates, and cestodes, and Group 4, indicated by isopods. This result suggests that solitary lifestyle hinders virus, apicomplexan, dinoflagellate, cestode, and isopod parasite groups.

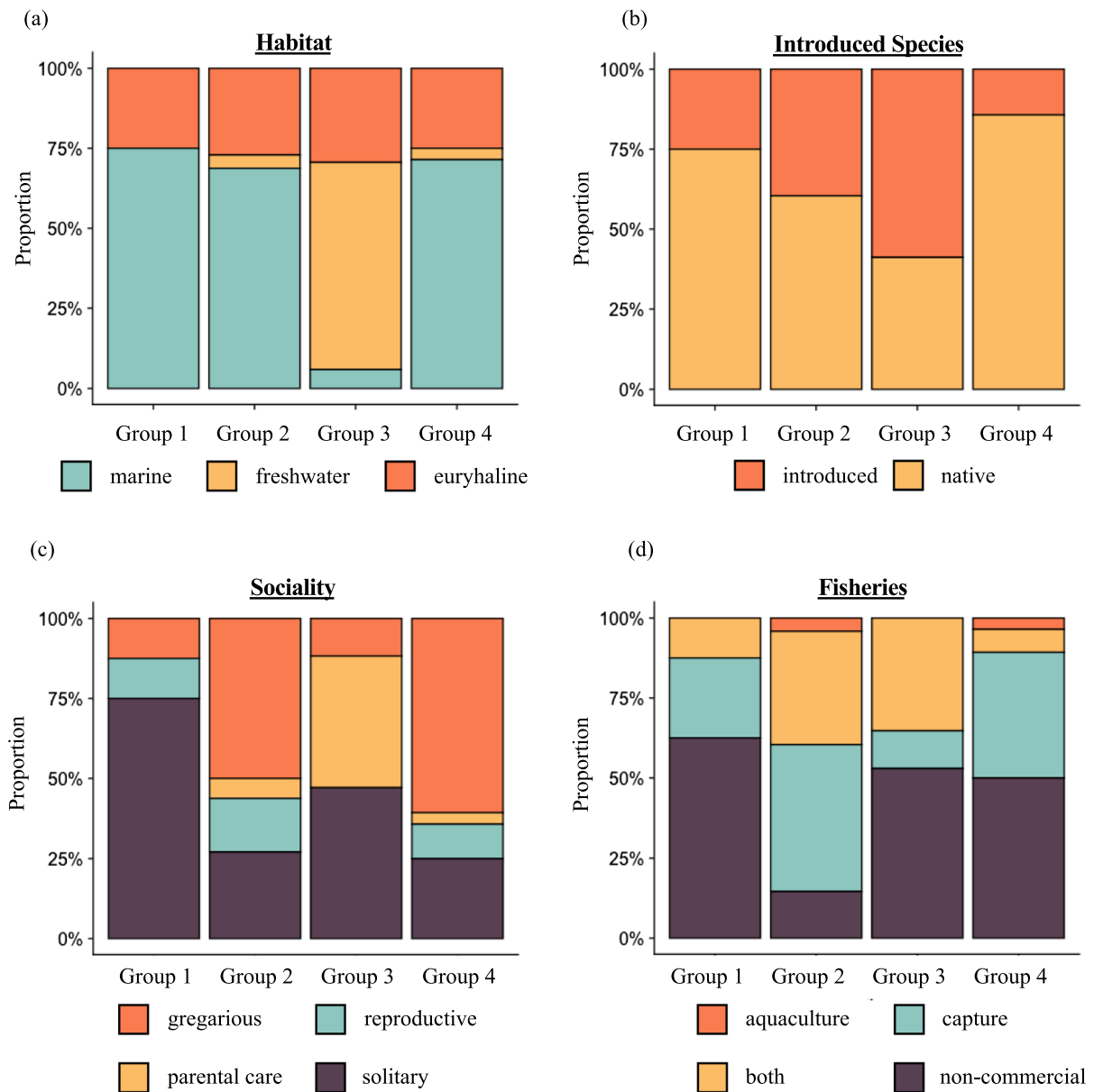


Fig. 7 Stacked bar charts showing the breakdown of host characteristics by polythetic agglomerative clusters, Groups 1–4. Host characteristics are **a** habitat, **b** introduced species, **c** sociality, and **d** fisheries exploitation

Hosts with parental care have significantly greater reported PSR than gregarious hosts ($F=11.9$, $df=3$, $p=0.008$; Fig. 8b) but neither are significantly different from solitary hosts or those with reproductive aggregations. Gregarious hosts would seem to have a greater opportunity to transmit parasites among conspecifics, which presents an opportunity for parasite diversification, and yet our data indicate that they

have reduced PSR. This pattern may be a result of evolved parasite avoidance behaviors, as exemplified by the gregarious Caribbean spiny lobster *P. argus* (Behringer et al. 2018), which aggregate with conspecifics using chemical cues (Anderson and Behringer 2013) but are also able to detect and avoid conspecifics infected with the pathogenic *Panulirus argus* virus 1 (PaV1) (Behringer et al. 2006; Subramaniam et al.

Fig. 8 A comparison of parasite species richness in decapod crustacean hosts by host characteristics: **a** habitat, **b** sociality, **c** introduced species, and **d** fishery exploitation. Lowercase letters above boxes indicate significant differences. Abbreviated outliers: *Cambarus bartonii*, *Paranephrops planifrons*, *Procambarus alleni*, *Austropotamobius torrentium*, *Macrobrachium nipponense*

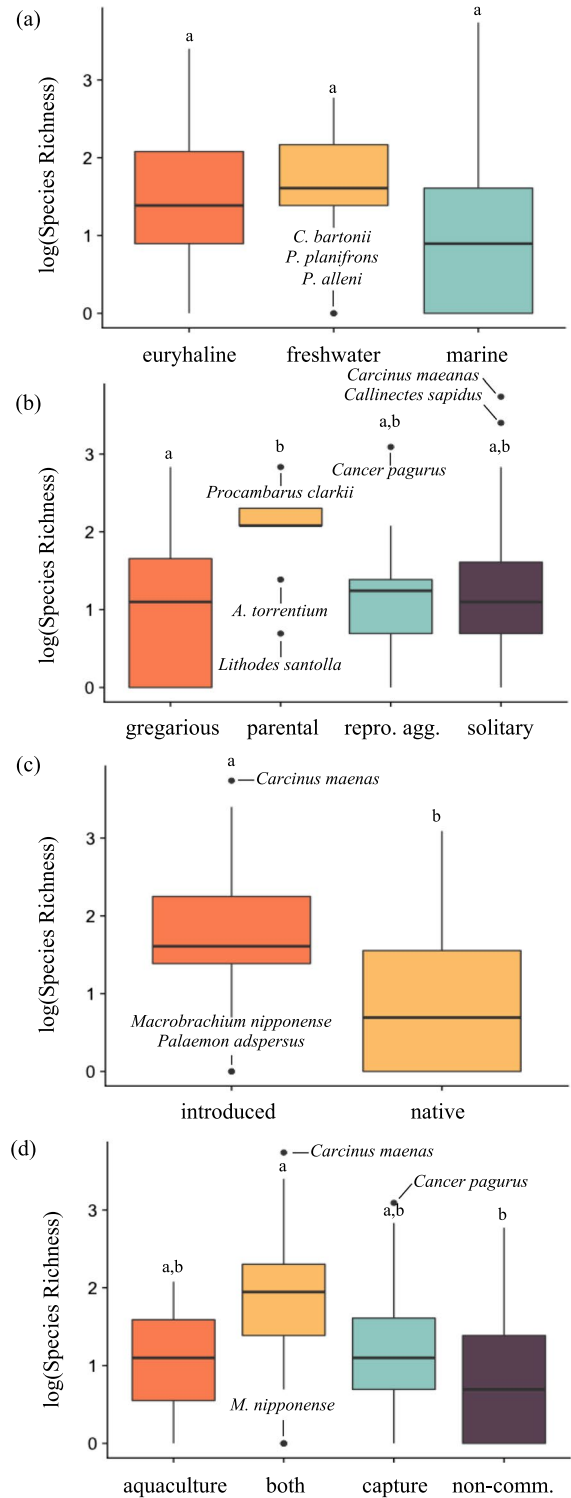
2020). Alternately, species with parental care would not benefit from avoiding a diseased parent or sibling, because they would be susceptible to much higher predation rates. This type of association could be utilized by directly transmitted parasites resulting in a diversity of parasites in this group.

Parasites in introduced hosts

Introduced species were not a significant discriminator in either the taxonomic LDA or agglomerative clustering LDA (Fig. 1; Fig. 7b), suggesting that being an INNS is not an important factor in the type of parasites that a decapod acquires. However, introduced species have significantly higher reported PSR ($F=18.1$, $df=1$, $p<0.001$; Fig. 8c) than native species. For introduced species, parasites were added to our dataset regardless of whether they were found in the native or introduced range and perhaps due to the range extent of introduction, the number of parasites encountered may increase. Thus, it is likely that both “parasite acquisition” in the invasive range and “enemy release” from many parasites in the native range are probably explanations for greater PSR in introduced species.

A further consideration in invasion biology is the potential spread of introduced parasites (spillover), which may also have the potential to infect animal/plant culture systems, fisheries, and native wildlife (Roy et al. 2017). Out of the updated list of crustacean invaders ($n=323$), it has been estimated that only 31.2% have at least one known symbiont, totaling 391 known symbionts (genus level or better) across the group (Bojko et al. 2021). Knowledge of such associations highlights the importance for informed legislation to limit their spread and impact (Foster et al. 2021).

The European shore crab, *Carcinus maenas*, is a destructive invader with 42 identified parasites in our dataset, though some estimates are higher (Bojko et al. 2018) and more are discovered regularly (Bojko et al. 2019; Subramaniam et al. 2020). This species



exemplifies both enemy release and parasite acquisition hypotheses, having 65 documented symbionts in its native range, 13 in both native and invasive range, and two species found in its invasive range only (Bojko et al. 2021). Release from the multitude of symbionts found only in its native range may have contributed to the shore crab's success as an invader – it has invaded coastal habitats worldwide (Torchin et al. 2001). Shore crabs have also acquired parasites, a microsporidian and a nemertean egg predator (Torchin et al. 1996; Bojko et al. 2017), in their North American invasive range—so far increasing the symbiont tally by two with many more portions of their invasive range remaining unscreened. The symbionts in both native and introduced ranges represent co-invasions with the crab and several are capable of spillover to infect alternative hosts, such as salmon and American lobster, within the invasive range (Bojko et al. 2018).

Parasites in aquaculture and commercial fisheries

In the taxonomic LDA there was a negative association between the non-commercial category and lobsters, meaning that lobsters and their parasites in our dataset are most predominant in capture fisheries (Fig. 1a). The amoebic parasite *Neoparamoeba pemaquidensis* of *H. americanus* provides a pertinent example of lobster parasitism affecting commercial capture fisheries. Paramoebiasis was implicated in a devastating fishery collapse in Long Island Sound in 1999 (Mullen et al. 2004, 2005). Between 1999 and 2002 the fishery was declared a commercial fishery failure by United States Congress and decreased in value from \$40 to \$7 million USD annually (Sears et al. 2022). It has yet to recover.

Decapods in both capture fisheries and aquaculture have greater reported PSR ($F=16.5$, $df=3$, $p<0.001$; Fig. 8d) than decapods not targeted by fisheries or aquaculture. This pattern likely relates to greater study efforts on fished hosts and greater interest and funding for determining causes of mortality. But parasites are also known to have interactive effects in fished ecosystems (Wood et al. 2010; Wood and Lafferty 2015). In general, PSR is reduced in areas where fishing occurs likely due to reduced host density, selective removal of the largest individual hosts, which tend to carry more parasites, and reduced food web complexity (Wood et al. 2014). The conditions

of aquaculture are known to promote viral and bacterial evolution. *Vibrio parahaemolyticus* is a common bacterial component of aquatic systems that acquired pathogenicity in aquaculture systems (Lee et al. 2015).

Parasitism and host sampling intensity

Host sampling intensity was not a significant factor in either taxonomic or agglomerative clustering LDAs, suggesting that this is not a strong differentiator of the groups and the types of parasites associated with them (Fig. 1). In the agglomerative clustering groups, Group 2 had significantly more citations than Group 1 and Group 4 ($F=6.9$, $df=2,97$, $p=0.0003$; Fig. 3b). There was also a significant positive relationship between the number of citations and reported PSR ($R^2=0.35$, $F=55.9$, $df=1,99$, $p<0.001$; Suppl. Fig. 2).

There are many concerns concerning ecological and economic implications of host-parasite relationships in crustaceans. The more we know about these relationships, the better we can identify and predict potential issues and guide aquaculture/fisheries management and choices. The study of parasites and disease should take a cue from the study of invasive species, where many government and research organizations are conducting “horizon scanning”, a systematic process to identify the risk associated with potential invasive species to a particular region (Therriault et al. 2008; Roy et al. 2014). Host species in Groups 1 and 4 offer a promising starting point for future studies because they are less well-studied than species in other groups.

Conclusions

Here we have presented the first synthesis of parasites in wild decapod crustaceans, with particular emphasis on fished and aquacultured species. Our analyses aimed to highlight patterns in available data as well as important data gaps. These patterns should not be interpreted as causal but rather correlations that deserve further examination. Below are our conclusions and recommendations.

- Most parasites were protozoan (18%) or viral (17%).

- Indicator species analysis revealed that crabs are indicated by rhizocephalans and dinoflagellates; crayfish are indicated by mesomycetozoans, oomycetes, branchiobdellids, and fungi; lobsters are indicated by copepods and amobae; shrimp were pseudo-indicated by viruses.
- Decapod species that are fished, aquacultured, introduced, exhibit parental care, or live in freshwater tend to have higher parasite species diversity.
- A solitary lifestyle hinders virus, apicomplexan, dinoflagellate, cestode, and isopod parasite groups and may be an ‘avoidance behavior’.
- Longevity was not a good predictor of parasite diversity or specific host-parasite relationships, but our dataset was biased to shorter-lived species, because accurately ageing crustaceans is difficult.
- Parasite diversity increased with how well-studied a host is. We recommend increased parasite screening in decapods and suggest this could be modeled after the horizon scanning approach used in invasion science.
- Similarly, we recommend addressing data gaps with methods aimed at highlighting biases such as the ERF and false negative analyses used here. These modeling approaches can be used to identify potential screening candidates, which can then be used to refine the model.
- The exclusion of geographic range data from these analyses is a significant caveat to our conclusions. Lack of reliable range data is an issue for nearly all marine organisms and collecting such information should be a focus of future research and collaboration. New technologies and techniques in remote sensing and ROVs, as well as curated databases to house this information could improve research in this area.

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Author contributions EDM and DCB—conceived of the study. EDM, JB, and NCS—compiled data. ZAS—performed false negative analysis, while EDM—performed remaining data analyses and figure development. All authors contributed to the development of the manuscript.

Data availability The data used to create this manuscript are available in Figshare with the identifier: <https://doi.org/https://doi.org/10.6084/m9.figshare.25513399>.

Declarations

Conflict of interest All authors certify that they have no relevant financial or non-financial interests to disclose.

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