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Jack Ingelbrecht

Karissa O. Lear

Storm B. Martin

Alan J. Lymbery

Bradley M. Norman

See next page for additional authors

Authors

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Ectoparasites of the Critically Endangered green sawfish *Pristis zijsron* and sympatric elasmobranchs in Western Australia

Jack Ingelbrecht [a,*], Karissa O. Lear [a], Storm B. Martin [a], Alan J. Lymbery [a], Bradley M. Norman [a], Geoffrey A. Boxshall [b], David L. Morgan [a,*]

[a] *Centre for Sustainable Aquatic Ecosystems, Harry Butler Institute, Murdoch University, 90 South Street, Murdoch, Western Australia 6150, Australia*
[b] *Department of Life Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom*

A B S T R A C T

This study reports the metazoan ectoparasite fauna of juvenile Critically Endangered green sawfish, *Pristis zijsron*, and sympatric elasmobranchs in Western Australia. Five parasite taxa were found on 76 screened *P. zijsron*: *Caligus furcisetifer* (Copepoda: Caligidae), *Dermopristis pterophila* (Monogenea: Microbothriidae), *Branchellion plicobranchus* and *Stibarobdella macrothela* (Hirudinea: Piscicolidae), and praniza larvae of an unidentified gnathiid isopod. Only *C. furcisetifer* and *D. pterophila* were common, exhibiting discrepant site-specificity, with *C. furcisetifer* occurring mostly on the head and rostrum, and *D. pterophila* around the pectoral and pelvic fins. Intensity of infection for *C. furcisetifer* and *D. pterophila* increased with host total length and was influenced by host sex, but in opposite directions; intensity of *C. furcisetifer* was greater on female *P. zijsron*, whereas intensity of *D. pterophila* was greater on males. In the Ashburton River, likelihood of infection for *C. furcisetifer* and *D. pterophila* on *P. zijsron* increased with time since substantial freshwater discharge events, suggesting decreased salinity impacts both taxa. In addition to *P. zijsron*, five other sympatric elasmobranch species were opportunistically screened for ectoparasites in the study area: the giant shovelnose ray, *Glaucostegus typus*, the eyebrow wedgefish, *Rhynchobatus palpebratus*, the nervous shark, *Carcharhinus cautus*, the lemon shark, *Negaprion acutidens*, and the graceful shark, *Carcharhinus amblyrhynchoides*. *Caligus furcisetifer* was found on *R. palpebratus*; no other parasites of *P. zijsron* were found on other sympatric elasmobranch species. Conversely, *Perissopus dentatus* (Copepoda: Pandaridae) was found on all three carcharhinids but not on batoid rays (*P. zijsron*, *G. typus* or *R. palpebratus*).

1. Introduction

Estimates of extinction rates and biodiversity loss usually fail to account for dependent symbionts, despite coextinctions accounting for most biodiversity loss [1–3]. Meaningfully including parasite taxa in biodiversity estimates and community models is challenging because most species are poorly known. For example, perhaps 85–95% of vertebrate helminth endoparasites remain unknown to science [4]. It is therefore important to characterise parasite faunas, particularly those of threatened host species, both to estimate potential biodiversity loss before a host becomes extinct and to understand the downstream community implications of parasite coextinctions.

The green sawfish, *Pristis zijsron* Bleeker, 1851 (Pristidae), is a large shark-like ray threatened with extinction primarily as a consequence of over-fishing [5,6,8]. Once distributed widely throughout the Indo-West Pacific, viable populations of *P. zijsron* are now mostly restricted to northern Australia [5,9–12], where it is listed as Vulnerable under the Environment Protection and Biodiversity Conservation Act 1999, whereas it is considered Critically Endangered both within Australia and globally, based on the International Union for Conservation of Nature Red List of Threatened Species classification criteria [6,7]. Northwestern Australia is a particularly important refuge for *P. zijsron* [10,13,14]. The Ashburton River delta in particular is an important nursery for *P. zijsron*; females pup reliably in spring each year and young remain within the sheltered waters of the estuary and associated tidal creeks throughout their juvenile phase [13,14]. The known parasite fauna of *P. zijsron* comprises six cestodes, one leech, one monogenean and one nematode [15–21]. Here we report on the ectoparasites occuring on *P. zijsron* in Western Australia, to characterise, and bring attention to, the previously unknown diversity of parasites infecting this

species in this region. Several other sympatric elasmobranchs were also screened for ectoparasites, to investigate host-specificity of parasites exploiting *P. zijsron*. Lastly, to investigate potential predictors of infection, we modelled parasite abundance in response to several abiotic and biotic factors, including the size and sex of the host and fluvial discharge.

2. Materials and methods

2.1. Host examination and parasite collection

Targeted sampling for *P. zijsron* was conducted in the Ashburton River mouth and associated mangrove creeks (Four Mile Creek, Hooley Creek and Hooley Lagoon/Ashburton Delta) in the Pilbara region of Western Australia. Supplementary, opportunistic sampling was conducted in the nearby Fortescue River estuary, as well as in the Bay of Rest in the Exmouth Gulf (Fig. 1; Table 1). *Pristis zijsron*, as well as other sympatric elasmobranchs (bycatch), were captured with monofilament gillnets or cast nets using methods detailed by Morgan et al. [13]. Upon capture, elasmobranchs were held on their backs in the extreme shallows with their gills submerged, inducing a state of tonic immobility, with sex and length (to the nearest mm) measured. Subsequent estimations of *P. zijsron* age classes were based on growth data reported by Lear et al. [22].

Examinations for ectoparasites were conducted first on the ventral surface, after which the host was righted for examination of the dorsal surface, before being released. Parasite attachment sites were recorded according to general body location: head (including rostrum, spiracles and nares), first and second dorsal fins (grouped together), pectoral fins, pelvic fins (including male reproductive organs, i.e., claspers), and caudal fin (including caudal peduncle). Ectoparasites were recorded as occurring on the dorsal or ventral body surface if they were not found on the head or on/adjacent to fins. Parasites were removed using forceps and immediately preserved in either 100% ethanol or 10% formalin. Measurements of water salinity were recorded within the Ashburton River and associated tidal creeks using a YSI Professional Plus Multi-parameter Meter (YSI Inc., Yellow Springs, United States of America) (Supplementary Table S1).

2.2. Morphological study

Parasite identifications were based solely on morphology, using primarily uncleared and unstained wet mounts in absolute ethanol. Specimens initially preserved in formalin were later transferred to absolute ethanol using a graded ethanol series: 40, 60, 75 and twice at 100%, for approximately 1 h per stage for mounting. Select copepod specimens were cleared in lactophenol and mounted (unstained) in Canada balsam. Monogeneans were treated as described previously (see Ingelbrecht et al. [20]). Slide-mounted specimens were examined and photographed using an Olympus BX50 compound microscope, with Nomarski interference contrast, fitted with an Olympus DP71 digital microscope camera and U-CMAD3 adaptor (Olympus Inc., Tokyo, Japan). Gnathiid isopods and piscicolid leeches were examined and photographed using an Olympus SZX7 stereo microscope with an Olympus DF PLAPO auxiliary lens.

2.3. Data analyses

Prevalence (proportion of infected hosts), intensity of infection (number of parasites per infected host) and parasite abundance (equivalent to prevalence × intensity) (mean and range) were calculated for each ectoparasite species across all screened *P. zijsron* and sympatric elasmobranchs, using the online tool QPweb (v. 1.0.15) [23]. Bias-corrected and accelerated bootstrap 95% confidence intervals (CI) were calculated for mean infection intensity. For ectoparasites with adequate sample sizes (i.e., present on ≥10 host individuals), aggregation was investigated in QPweb from variance/mean ratios (s^2/m) and negative binomial exponent values (k), with aggregation indices calculated across all screened *P. zijsron*. Aggregation was not investigated for ectoparasites found on sympatric elasmobranchs, because of inadequate
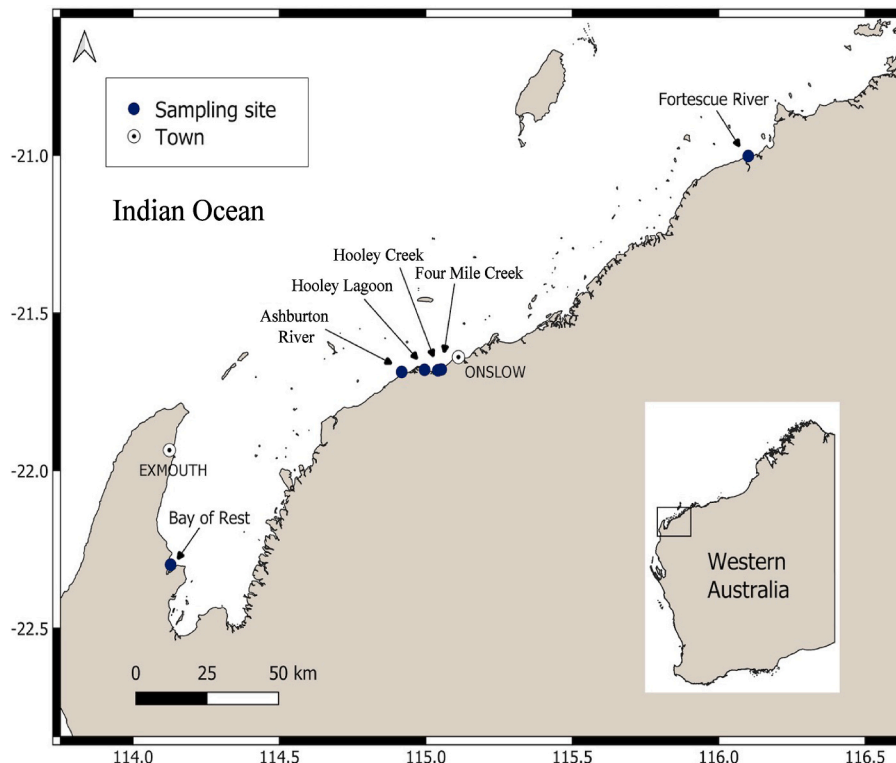

Fig. 1. Sampling locations for green sawfish, *Pristis zijsron* Bleeker, 1851, in Western Australia.

Table 1

Catch data for green sawfish, *Pristis zijsron*, screened for ectoparasites in Western Australia.

Site	Coordinates		n	Sex		TL (mm)	Age class		Capture date
	Lat°	Lon°		F	M		YOY	≥1+	
AR	−21.694	114.917	35	17	18	651–3195	23	12	10/2019–10/2022
BR	−22.321	114.119	3	0	3	804–843	3	0	09/2021
FM	−21.683	115.056	12	5	7	810–1988	10	2	04/2021–10/2022
FR	−21.006	116.099	3	0	3	790–2015	1	2	08/2022
HC	−21.687	115.036	6	3	3	832–1532	5	1	04/2021–10/2022
HL	−21.676	114.985	17	12	5	789–2195	13	4	10/2020–10/2022

Abbreviations: AR, Ashburton River estuary; BR, Bay of Rest; FM, Four Mile Creek; FR, Fortescue River; HC, Hooley Creek; HL, Hooley Lagoon/Ashburton Delta; F, female; M, male; TL, total length; YOY, young of the year; ≥1+, juveniles that are one year and older.

Age classes are based on Lear et al. [22].

sample sizes (i.e., present on <10 host individuals).

For ectoparasites encountered on at least 10 host individuals, site-specificity was investigated in QPweb by comparing the number of specimens found on or adjacent to infection sites. Bias-corrected and accelerated bootstrap 95% CI were calculated for mean parasite abundance for each infection site. No correction was applied to control for discrepancy in available surface area between site categories, because data for host surface areas were not available. Differences in parasite abundance between attachment sites were compared using a bootstrap one-way ANOVA test with 2000 bootstrap replications. The relationship between infection site usage and parasite intensity was investigated using Spearman's Rank correlation coefficient (r), by comparing the number of infection sites occupied by a species with intraspecific intensity, based on 10000 Monte Carlo replications.

Predictors of parasite abundance were examined using a series of models in R (v. 4.2.3; R Foundation for Statistical Computing, Vienna, Austria). Because parasite abundances were aggregated among hosts (see Results), we compared several distributions to account for over-dispersion, including negative binomial, zero-inflated negative binomial and zero-inflated Poisson. Fixed predictors of abundance incorporated into initial models included host stretched total length (TL) and sex, and time since substantial fluvial discharge in the Ashburton River, measured as the number of days since discharge fell below 10 ML day^{-1}. Discharge information was obtained from the Nanutarra Station [24] (situated >150 km upstream of the Ashburton River mouth). Freshwater is typically lethal to marine ectoparasites [25–27]. We used time since substantial river discharge to the estuary as an indication of exposure to freshwater, rather than direct measurements of salinity, because one-off salinity measurements are unlikely to accurately reflect recent environmental exposure for large juvenile *P. zijsron*, which are known to be transient. Sampling location was not incorporated as a predictor in models, because several localities (50%) had few samples (i.e., <10 screened *P. zijsron*). Models using all combinations of predictor variables and model types were created. The best-fit model from this set was chosen through examination of Akaike's Information Criterion (AIC), where the best-fit model was selected as the model with the lowest AIC score, or, if the lowest AIC scores were within two AIC units of each other, selected as the model with the fewest degrees of freedom (DF).

3. Results

3.1. Elasmobranchs

A total of 76 juvenile *P. zijsron* (37 females, 39 males) were examined for ectoparasites (Table 1). Of these, ectoparasites were detected on 43 individuals. A further five elasmobranch species were opportunistically screened for ectoparasites in the Ashburton River estuary and associated tidal creeks: the giant shovelnose ray, *Glaucostegus typus* (Anonymous [Bennett], 1830) (Glaucostegidae) ($n = 16$), the eyebrow wedgefish, *Rhynchobatus palpebratus* Compagno & Last, 2008 (Rhinobatidae) ($n = 4$), the graceful shark, *Carcharhinus amblyrhynchoides* (Valenciennes,

1839) (Carcharhinidae) ($n = 2$), the nervous shark, *Carcharhinus cautus* (Whitley, 1945) (Carcharhinidae) ($n = 24$), and the lemon shark, *Negaprion acutidens* (Rüppell, 1837) (Carcharhinidae) ($n = 6$) (Table 2).

3.2. Parasite taxa

Five ectoparasitic taxa were detected on *P. zijsron*: *Caligus furcisetifer* Redkar, Rangnekar & Murti, 1949 (Copepoda: Caligidae), *Dermopristis pterophila* Ingelbrecht, Morgan & Martin, 2022 emend. (Monogenea: Microbothriidae), *Branchellion plicobranchus* Sanjeeva Raj, 1953 and *Stibarobdella macrothela* (Schmarda, 1861) (Hirudinida: Piscicolidae), and an unidentified gnathiid encountered as praniza larvae (Isopoda: Gnathiidae; referred to as Gnathiidae gen. sp.) (Table 3). Ectoparasites were predominantly encountered at low prevalences (i.e., encountered on <10 host individuals). *Caligus furcisetifer* (Fig. 2) and *D. pterophila* (Fig. 3) were the only species observed on >10% of *P. zijsron*, observed on 39% and 32% of *P. zijsron*, respectively. Leeches and gnathiids were consistently scarce, with only two *B. plicobranchus* (Fig. 4), five *S. macrothela* (Fig. 5), and eight Gnathiidae gen. sp. (Fig. 6) encountered during screenings.

Caligus furcisetifer was also detected on the snout and pectoral fins of two *R. palpebratus* (Table 4). No other ectoparasite species encountered on *P. zijsron* was found on any sympatric elasmobranch species. However, another copepod species, *Perissopus dentatus* Steenstrup & Lütken, 1861 (Pandaridae) (Fig. 7), was found on one *C. amblyrhynchoides*, eight *C. cautus* and three *N. acutidens*, and was the only ectoparasite detected on these carcharhinids.

Lastly, egg tracks from an unidentified parasite (likely a nematode)

Table 2

Catch data for elasmobranchs screened for ectoparasites while surveying green sawfish, *Pristis zijsron*, in the Ashburton River estuary and adjacent tidal creeks, Western Australia.

Species	n	Sex		TL (mm)	Site	Capture date
		F	M			
Carcharhinus amblyrhynchoides	2	1	1	1243–1251	AR	10/2020–04/2021
Carcharhinus cautus	24	17	7	688–1148	AR, FM, HC, HL	10/2020–10/2022
Glaucostegus typus	16	7	7	432–595	AR, FM, HC, HL	10/2020–04/2021
Negaprion acutidens	6	2	4	645–1216	AR, FM, HC, HL	10/2020–10/2022
Rhynchobatus palpebratus	4	3	1	1468–1764	AR	10/2020–10/2021

Abbreviations: AR, Ashburton River estuary; FM, Four Mile Creek; HC, Hooley Creek; HL, Hooley Lagoon/Ashburton Delta; F, female; M, male; TL, total length. Host sex data were not recorded for two *G. typus*.

Table 3
Ectoparasites infecting green sawfish, *Pristis zijsron*, in Western Australia.

Parasite	Prevalence	Intensity	Infection site	Locality
Caligidae				
Caligus furcisetifer	39 (30)	1–54 (7.5; 4.7–15.7)	hd; df; pc; cf; ds	AR; BR; FM; FR; HL
Gnathiidae				
Gnathiidae gen. sp.	5 (4)	1–4 (2; 1.3–3.3)	nr	FM
Microbothriidae				
Dermopristis pterophila	32 (24)	1–13 (2.2; 3.3–6.3)	hd; df; pc; pv; cf; ds; vs	AR; FM; HC; HL
Piscicolidae				
Branchellion plicobranchus	3 (2)	1	cf (open wound); nr	AR
Stibarobdella macrothela	3 (2)	1–4 (2.5; 1.0–2.5)	hd; nr	BR; FR

Abbreviations: AR, Ashburton River estuary; BR, Bay of Rest; FM, Four Mile Creek; FR, Fortescue River; HC, Hooley Creek; HL, Hooley Lagoon/Ashburton Delta; cf, caudal fin (including peduncle); df, dorsal fins; ds, dorsal body surface not in proximity to fins; hd, head; nr, nares; pc, pectoral fins; pv, pelvic fins (including male reproductive organs); vs, ventral body surface not in proximity to fins.

Prevalence is the percentage of hosts infected, followed by the number of hosts infected in parentheses, out of 76 screened *P. zijsron*. Intensity is the range of intensity of infection, followed by the mean and 95% confidence intervals in parentheses.

were observed on the snout, adjacent to the gills and on the pectoral fins of a single *G. typus* (597 mm TL) captured in Hooley Lagoon. No scrapings were taken of these tracks, nor were any similar tracks observed on *P. zijsron*.

3.2.1. *Caligus furcisetifer*

Caligus furcisetifer is one of few caligids known to parasitise elasmobranchs [28–30]. Our identification is consistent with previous reports [29–31] on the basis of the following: body size (4.5–5.0 mm body length; $n = 5$); shape and details of the cephalothorax, rounded, approximately 1.1 times longer than wide, with maximum width approximately half of the distance from the anterior end, comprising approximately 65% of total body length (Fig. 2b), and presence of a small, triangular sclerite on the ventral surface that projects distally over dentiform process base of the maxillule; details of the genital complex, approximately 1.3 times wider than long, with rounded corners; size and position of lunules, minute and shifted laterally on the frontal plate (Fig. 2c); presence of an accessory process on middle and inner terminal spines and reduced apical seta on the terminal exopodal segment of leg 1 (Fig. 2e); and subequal middle and outer spines on the terminal exopodal segment of leg 4 (Fig. 2f). This species has previously been reported from an unidentified *Pristis* species in Indian coastal waters, from the largetooth sawfish, *Pristis pristis* (Linnaeus, 1758) (formerly *P. microdon*), in northern Australia, from *G. typus* in Moreton Bay, Queensland, from the grey nurse shark, *Carcharias taurus* Rafinesque,
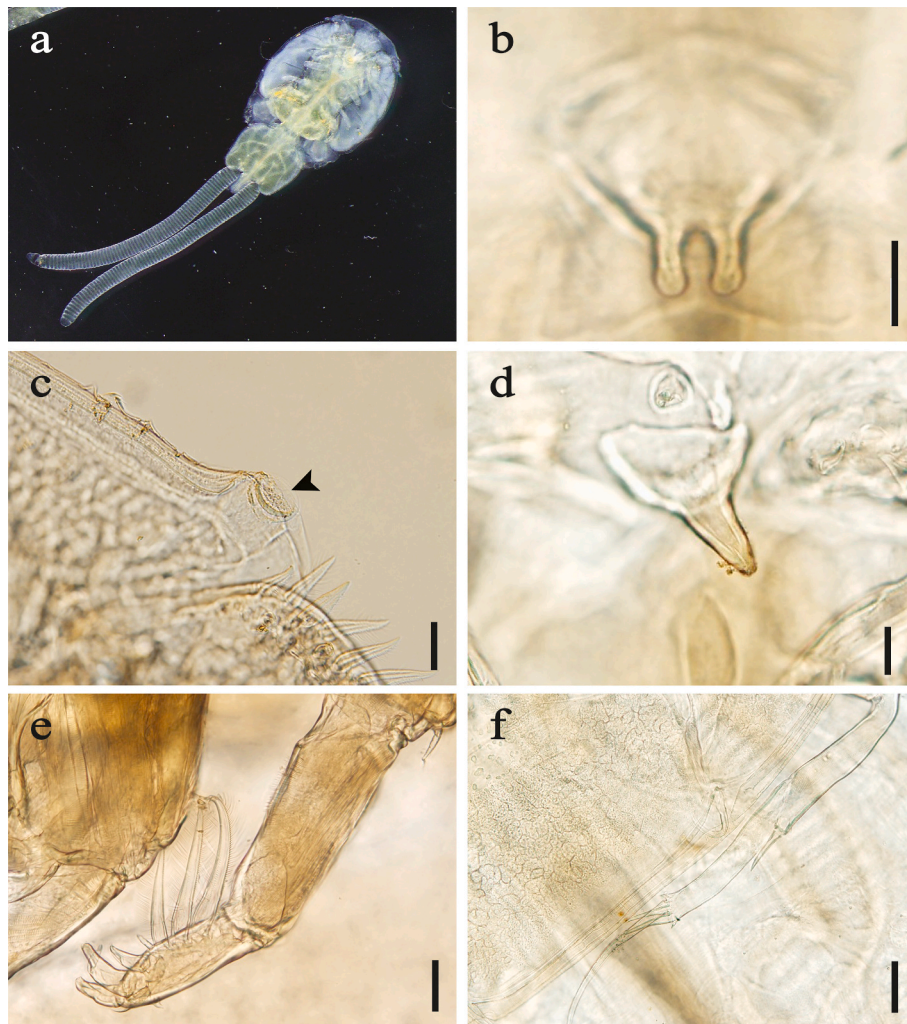

Fig. 2. Female *Caligus furcisetifer* Redkar, Rangnekar & Murti, 1949 (Copepoda: Caligidae), from the skin of the green sawfish, *Pristis zijsron* Bleeker, 1851, in Western Australia. (a) Habitus, dorsal view. (b) Sternal furca. (c) Left lunule. (d) Left maxillule. (e) Left leg 1 exopod. (f) Left leg 4 exopod. Scale bars: b–f = 50 μm.
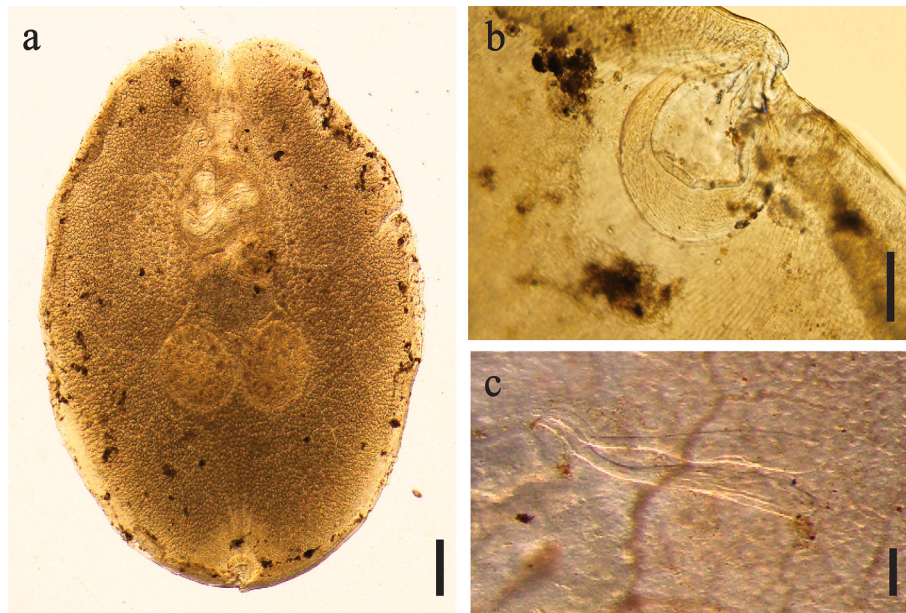
Fig. 3. *Dermopristis pterophila* Ingelbrecht, Morgan & Martin, 2022 (Monogenea: Microbothriidae), from the skin of the green sawfish, *Pristis zijsron* Bleeker, 1851, in the Ashburton River, Western Australia. (a) Habitus, ventral view. (b) Simple haptor. (c) Spermatophore capsules. Scale bars: a = 500 μm; b, c = 100 μm.
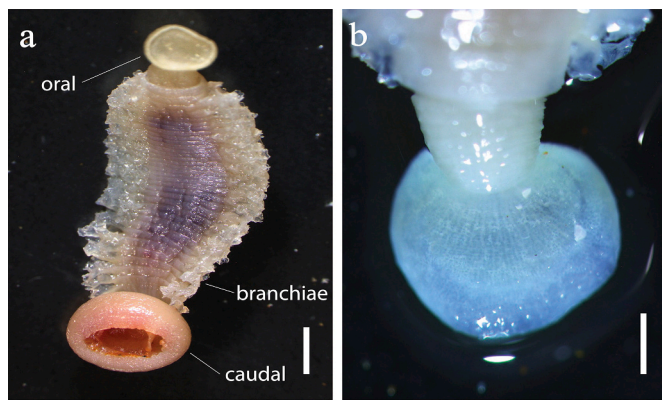

Fig. 4. *Branchellion plicobranchus* Sanjeeva Raj, 1953 (Hirudinida: Piscicolidae), from the skin of the green sawfish, *Pristis zijsron* Bleeker, 1851, in the Ashburton River, Western Australia. (a) Habitus, ventral view, showing lateral branchiae. (b) Oral sucker, dorsal view. Scale bars: a = 2 mm; b = 500 μm.

1810, in Jeffreys Bay and from the bull shark, *Carcharhinus leucas* (Valenciennes, 1839), in Kwazulu-Natal, South Africa [29,30,32]. *Caligus furcisetifer* was found on *P. zijsron* at all sampling locations except for Hooley Creek (Table 3) and on *R. palpebratus* in the Ashburton River estuary, which are the first records of *C. furcisetifer* occuring on these host species. These records extend the geographical range of *C. furcisetifer* south in the eastern Indian Ocean to the Exmouth Gulf, Western Australia.

3.2.2. *Dermopristis pterophila*

The morphology of the microbothriids recovered here is consistent with those of *Dermopristis pterophila*, which we justified previously in Ingelbrecht et al. [20]. *Dermopristis pterophila* seemingly has a narrow geographic range and, like its congeners, is believed to be host-specific, known only from *P. zijsron* in the Ashburton River estuary and adjacent tidal creeks [20,33,34].

3.2.3. *Branchellion plicobranchus* & *Stibarobdella macrothela*

Species of *Branchellion* Savigny, 1822, are smooth, non-tuburculate
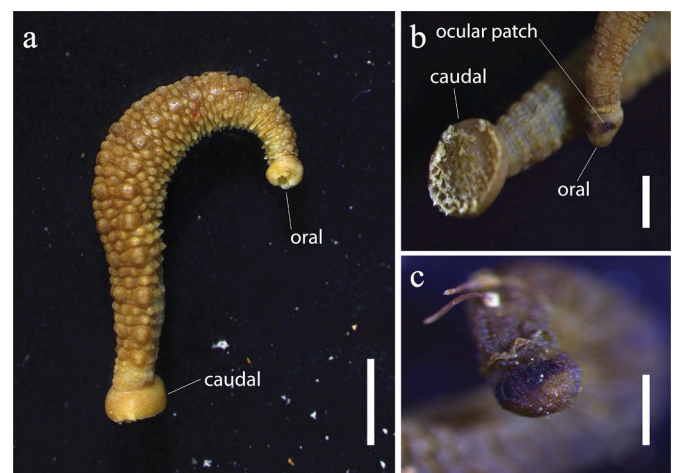

Fig. 5. *Stibarobdella macrothela* (Schmarda, 1861) (Hirudinida: Piscicolidae) from the skin of the green sawfish, *Pristis zijsron* Bleeker, 1851, in the Fortescue River, Western Australia. (a) Habitus, lateral view. (b) Oral sucker showing ocular patches and caudal sucker. (c) Contracted oral sucker, lateral view. Scale bars: a = 2 mm; b, c = 500 μm.

leeches, with three species known from Australian waters: *Branchellion australis* Legih-Sharpe, 1916, which is known from southern Australia and from Shark Bay, Western Australia (over 400 km southwest of Onslow); *Branchellion lineare* Baird, 1869, known from King Sound near Derby, Western Australia; and *B. plicobranchus,* known from eastern Australia, including from a "shovelnose" in Moreton Bay, Queensland (likely *G. typus*) [21,35]. Our specimens, which were found only on *P. zijsron* in the Ashburton River estuary (Table 3), are consistent with *B. plicobranchus*, based on the 33 pairs of leaf-like branchiae (Fig. 4a), absence of eyespots on the oral sucker, and absence of an obvious bilobed hump on the ventral surface of segment VII [36].

Species of *Stibarobdella* Leigh-Sharpe, 1925, are large, tuburculate leeches that are known only from elasmobranchs, including *P. zijsron* in the Embley River, Queensland [21,37,38]. Our specimens, which were found only on *P. zijsron* in the Bay of Rest and Fortescue River, are consistent with *S. macrothela* (previously *Pontobdella macrothela*), based
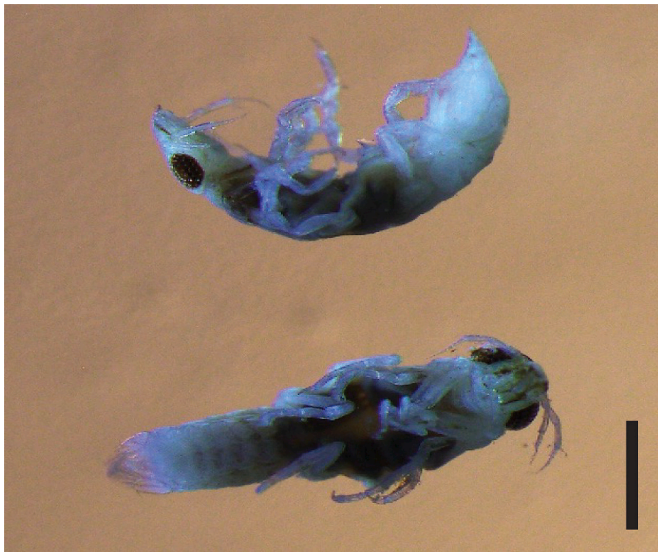
Fig. 6. Gnathiidae gen. sp. from the nares of the green sawfish, *Pristis zijsron* Bleeker, 1851, in the Ashburton River, Western Australia; lateral (top) and ventral (bottom) views. Scale bar = 1 mm.

on the large, wart-like tubercles present both dorsally and ventrally on each annulus of each trachelosome and urosome segment (Fig. 5a), two large, trumpet-shaped ocular patches on the oral sucker (Fig. 5b), and a large caudal sucker [21,39].

3.2.4. Gnathiidae gen. sp.

Although over 100 species of gnathiids are known from Australian waters [40,41], including from numerous elasmobranchs in northern Australia [41,42], this is the first record of a gnathiid parasitising a pristid, worldwide. Gnathiid taxonomy is typically based on adult males [43], and therefore, we have not made efforts to determine the specific identity of pranizae recovered here. Our specimens were found only on *P. zijsron* in Four Mile Creek and are consistent with gnathiid morphology on the basis of the following: body size (4.0–4.3 mm body length; $n = 4$); cephalosome with well-developed, ovoid compound eyes on the lateral margins, straight medio-anterior margins possessing concave lateral excavations, posterior cephalosome margin wider than anterior margin, presenting few setae on the posterior dorsal region, first antenna being shorter than second antenna and antenna 1 having three pedunculate articles; peraeon being larger than cephalosome, with perionite 1 fused with cephalon, and with shallow, convex anterior and posterior borders; and triangular-shaped pleotelson, with straight lateral marins, longer than it is wide, presence of two simple setae on the dorsal surface, and distal tip ending in pair of setae (Fig. 6) [44].

3.2.5. Perissopus dentatus

Perissopus dentatus has perhaps the broadest host-range of any pandarid, known from over 30 elasmobranchs, mostly carcharhinids

[45,46]. Our identification of *P. dentatus*, based on the morphology of female specimens, is consistent with previous reports on the basis of the following: body size (4.1–4.5 mm body length; $n = 3$); anteriorly narrow cephalothorax, widest at posterior margins; dorsal plates of thoracic segments rounded, with crenate posterior margins; dorsal plates of second thoracic segment oblique; dorsal plates of third thoracic segment slightly overlapping along the mid-line; presence of adhesion pads, all legs lacking plumose setae; genital segment larger than cephalothorax, with pair of postero-lateral processes; and a pair of posterior lobes with crenate hind margins [45,47]. This species has previously been reported from Australian waters in Cleveland Bay, Queensland, from the creek whaler, *Carcharhinus fitzroyensis* (Whitley, 1943), the spot-tail shark, *Carcharhinus sorrah* (Valenciennes, 1839), the whitecheek shark, *Carcharhinus dussumieri* (Valenciennes, 1839), and the scalloped hammerhead, *Sphyrna lewini* (Griffith & Smith, 1834) [48]. To our knowledge, this is the first record of *P. dentatus* parasitising *C. amblyrhynchoides*, *C. cautus* and *N. acutidens*, and the first record from Western Australia.

3.3. Aggregation, prevalence and intensity of Caligus furcisetifer and Dermopristis pterophila

Caligus furcisetifer and *D. pterophila* were both highly aggregated on *P. zijsron* ($s^2/m = 27.96$, $k = 0.15$; $s^2/m = 6.05$, $k = 0.18$, respectively). Akaike's Information Criterion values indicated a zero-inflated negative binomial model type was the best-fit for *C. furcisetifer* (AIC = 186.96, DF
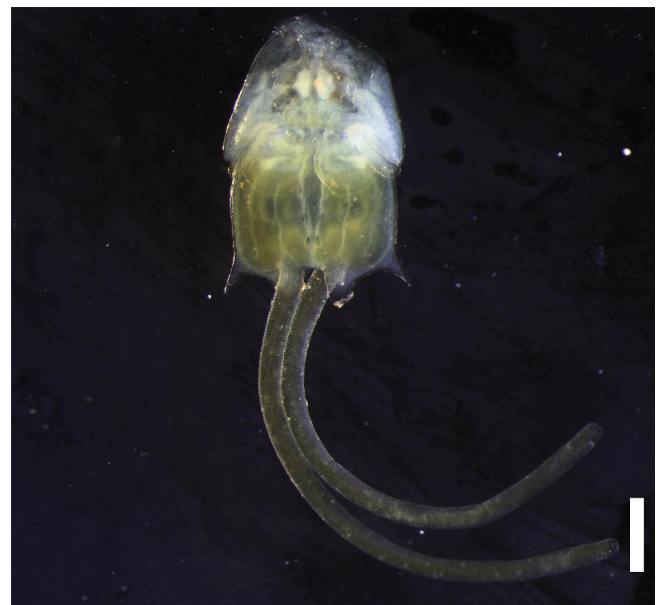

Fig. 7. *Perissopus dentatus* Steenstrup & Lütken, 1861 (Copepoda: Pandaridae), from the skin of the nervous shark, *Carcharhinus cautus* (Whitley, 1945), in the Ashburton River, Western Australia; habitus, dorsal view. Scale bar = 1 mm.

Table 4
Ectoparasites infecting elasmobranchs caught as bycatch while surveying green sawfish, *Pristis zijsron*, in the Ashburton River estuary and adjacent tidal creeks, Western Australia.

Host	n	Parasite	Prevalence	Intensity	Infection site	Locality
Carcharhinus amblyrhynchoides	2	*Perissopus dentatus*	50 (1)	2	cf	AR
Carcharhinus cautus	24	*Perissopus dentatus*	33 (8)	1–4 (2.1; 1.4–2.8)	af; cf; cls; df; pc	AR; FM; HC; HL
Negaprion acutidens	6	*Perissopus dentatus*	50 (3)	1–2 (1.7; 1.0–2.0)	cf; df	AR; FM; HL
Rhynchobatus palpebratus	4	*Caligus furcisetifer*	50 (2)	1–7 (4; 1.0–4.0)	pc; sn	AR

Abbreviations: AR, Ashburton River estuary; FM, Four Mile Creek; HC, Hooley Creek; HL, Hooley Lagoon/Ashburton Delta; af, anal fin; cf, caudal fin; cls, claspers; df, dorsal fins; pc, pectoral fins; sn, snout.

Prevalence is the percentage of hosts infected, followed by the number of hosts infected in parentheses. Intensity is the range of intensity of infection, followed by the mean and 95% confidence intervals in parentheses.

= 9), whereas a zero-inflated Poisson model type was the best-fit for *D. pterophila* (AIC = 171.05, DF = 8) (Supplementary Table S2). Zero-inflated models assume that excess zeros are generated by a separate process from count data and are therefore modelled separately; in this case, the first modelled distribution relates to the odds of infection for a host (i.e. whether it is infected or not), and the second relates to the intensity of infection. The best-fit model for *C. furcisetifer* included host TL, host sex, and days since water discharge fell below 10 ML day^{-1} as predictors of parasite presence (AIC = 187.37, DF = 8), with odds of infection increasing with host TL and days since discharge fell below 10 ML day^{-1}, and females more likely to be infected than males (Supplementary Table S3). Host TL and sex were the best predictors of infection intensity (AIC = 187.37, DF = 8), which increased with TL, and female *P. zijsron* were more heavily infected than males, especially females >2500 mm TL (Fig. 8) (Supplementary Table S4).

For *D. pterophila*, host TL and days since water discharge fell below 10 ML day^{-1} were maintained as predictors of parasite presence in the best-fit model (AIC = 172.87, DF = 6) (Supplementary Table S3), with the odds of infection increasing with host TL and with days since discharge fell below 10 ML day^{-1}. The best-fit predictors of *D. pterophila* infection intensity were host TL and sex (AIC = 172.87, DF = 6) (Supplementary Table S4). Intensity increased with *P. zijsron* TL and, in

contrast to *C. furcisetifer*, male *P. zijsron* were more heavily infected than females, although the effect was not as compelling as for *C. furcisetifer*, and pertained mostly to hosts >2500 mm TL (Fig. 8).

3.4. Site specificity

There were significant differences in the mean number of both *C. furcisetifer* ($P = 0.047$) and *D. pterophila* ($P = 0.001$) between infection sites on *P. zijsron*. *Caligus furcisetifer* were found predominantly on the head and rostrum (mean = 7.73 *C. furcisetifer* per infected *P. zijsron*; 95% CI = 4.27–15.20), with small numbers of copepods found on, or adjacent to, the dorsal fins (mean = 0.23; 95% CI = 0.03–0.83), pelvic fins (mean = 0.07; 95% CI = 0.01–0.20), caudal fin and peduncle (mean = 0.20; 95% CI = 0.03–0.63), and on the general dorsal body surface (mean = 0.40; 95% CI = 0.03–1.46). No copepods were encountered on, or adjacent to, the pectoral fins, nor on the general ventral body surface (Fig. 9). Number of infection sites used by *C. furcisetifer* increased with copepod infection intensity ($r = 0.54$, $P <0.0001$), with only one site (head and rostrum) used when nine or fewer copepods were present and up to three sites used at an intensity of 10 copepods.

Dermopristis pterophila were found almost exclusively posterior to the gills of their host, with only a single specimen found anterior to
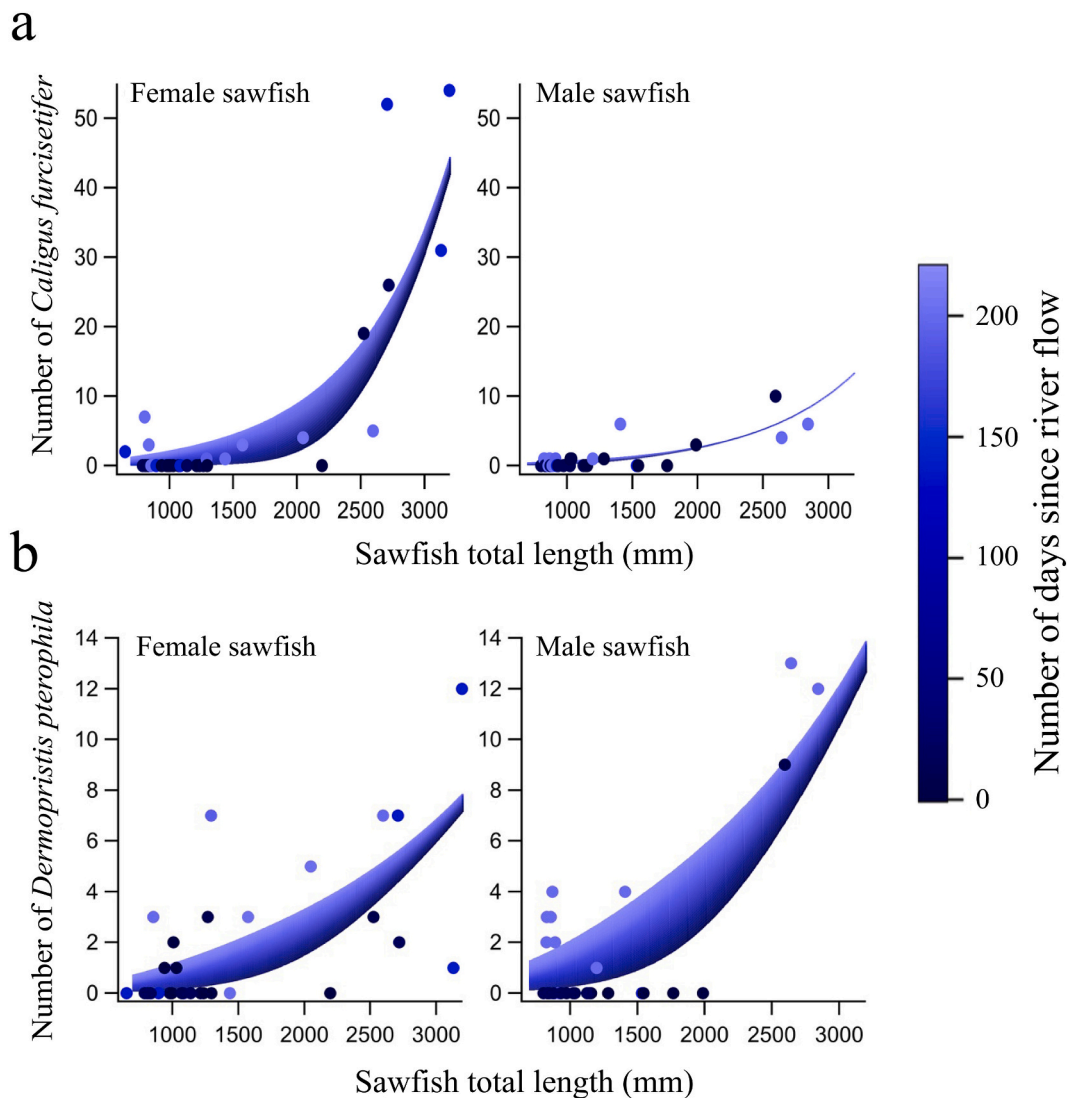

Fig. 8. Abundance (data points) and model-predicted intensity (curve) of (a) *Caligus furcisetifer* Redkar, Rangnekar & Murti, 1949, and (b) *Dermopristis pterophila* Ingelbrecht, Morgan & Martin, 2022, on the green sawfish, *Pristis zijsron* Bleeker, 1851 ($n = 70$), in the Ashburton River and adjacent tidal creeks, Western Australia. Abundance is displayed relative to host total length (mm), sex, and number of days since river discharge fell below 10 ML day^{-1}.
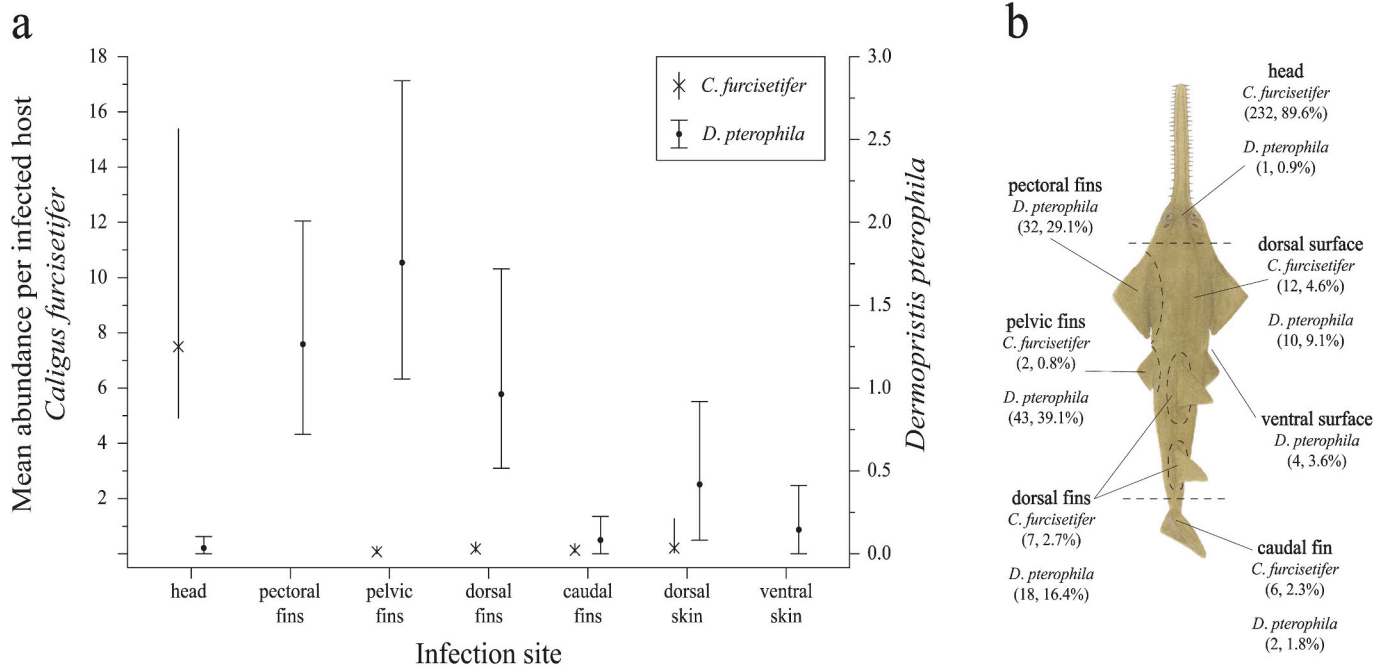
Fig. 9. (a) Mean abundance with 95% confidence intervals of *Caligus furcisetifer* Redkar, Rangnekar & Murti, 1949, and *Dermopristis pterophila* Ingelbrecht, Morgan & Martin, 2022, on or adjacent to one of seven sites of infection on the green sawfish, *Pristis zijsron* Bleeker, 1851, infected with at least one *C. furcisetifer* (*n* = 30 *P. zijsron*) and/or *D. pterophila* (*n* = 24 *P. zijsron*) in Western Australia. (b) Gross morphology of *P. zijsron* with combined total numbers of individual *C. furcisetifer* or *D. pterophila*, per infection site, and the site prevalence (%) of each taxon calculated out of the total number of hosts infected with at least one *C. furcisetifer* or *D. pterophila*. *Caligus furcisetifer* was not encountered on the pectoral fins or isolated on the ventral surface. Head includes body surface anterior to the gills; caudal fin includes caudal peduncle; pelvic fins include male reproductive organs (claspers). Illustration by K.O. Lear.

respiratory organs. The number of *D. pterophila* infections was greatest on, or immediately adjacent to, the pelvic fins (mean = 1.79 *D. pterophila* per infected *P. zijsron*; 95% CI = 1.11–2.96), with moderate numbers of worms recorded on, or adjacent to, the pectoral fins (mean = 1.33; 95% CI = 0.75–2.12) and dorsal fins (mean = 0.75; 95% CI = 0.38–1.21), and few on the head/rostrum (mean = 0.04; 95% CI = 0.01–0.13), caudal fin and peduncle (mean = 0.08; 95% CI = 0.01–0.21), or elsewhere on either the dorsal (mean = 0.42; 95% CI = 0.08–1.00) or ventral (mean = 0.17; 95% CI = 0.01–0.38) body surfaces (Fig. 9). Number of infection sites used by *D. pterophila* increased with worm infection intensity (*r* = 0.77, *P* <0.0001), with sites other than the pelvic fins used at an intensity of three worms and a maximum of five sites used at an intensity of 12 worms.

Gnathiidae gen. sp., *Branchellion plicobranchus* and *S. macrothela* were encountered too infrequently for statistical analyses of site preference, but Gnathiidae gen. sp. occurred exclusively in host nares, the two *B. plicobranchus* were found in a naris and on an open wound on the caudal peduncle, and *S. macrothela* were found exclusively in host nares or elsewhere on the head.

4. Discussion

Chondrichthyan metazoan parasites are an important component of biodiversity, and may inform several aspects of their host's biology, geographical origins, phylogeny, and migrations [49–51]. This research has increased the number of species reported for *P. zijsron* by three metazoan taxa, bringing the known parasite fauna for this host to 12 metazoan taxa.

4.1. Aggregation and patterns of ectoparasite presence and intensity

Generally, host individuals are infected with few or no parasites of a given species, whereas a small proportion of individuals are infected with many parasites [52–54]. The aggregated distribution of *C.*

furcisetifer and *D. pterophila* found here (*k* <1) is typical among parasite populations [54–56] and could be the consequence of a number of factors, such as heterogeneity in individual host exposure to infection, host susceptibility to infection, and parasite choice of host [56–58]. However, to determine the relative importance of these factors, additional work is required, such as relating host condition and immunocompetence to parasite abundance [59].

In our analyses, the best-fit models demonstrated that larger *P. zijsron* are more likely to be infected and carry a greater intensity of infection for both *C. furcisetifer* and *D. pterophila*. Correlations between host size and parasite intensity are common and intuitive; larger, older fish have had more time to accumulate parasites and offer greater surface area for parasites to colonise [60–62]. This pattern has also been reported for numerous other marine fishes [60,63,64], including for the microbothriid *Dermophthirioides pristidis* Cheung & Nigrelli, 1983, on the smalltooth sawfish, *Pristis pectinata* Latham, 1974, off the coast of Florida, USA [65]. Furthermore, larger juveniles of *P. zijsron* are known to expand their home ranges [14], likely increasing their chances of accruing more infections than smaller individuals [66]. Although smaller *P. zijsron* were less frequently infected and carried less parasite loads, even some of the smallest juveniles surveyed were infected (≥651 mm TL; estimated as being neonates due to the presence of a fresh yolk sac scar). It is therefore plausible that newborn *P. zijsron* might occasionally acquire infections from their mother during birth, although we cannot discount acquisition from associating with older juveniles.

For *C. furcisetifer* and *D. pterophila*, infection prevalence and intensity increased with time since substantial fluvial discharge. Freshwater exposure is lethal to caligids and monogeneans, and in mariculture, freshwater bathing is a highly effective treatment for marine ectoparasites [25–27,67–70]. Furthermore, salinity in the Ashburton River estuary is variable and fluvial discharge is non-existent throughout most of the year, occuring only after precipitation, when salinity declines briefly (see Supplementary Table S1) [71]. *Pristis zijsron* appear to temporarily leave the Ashburton River estuary for nearby, more saline environments

following periods of significant precipitation [14], which may afford parasites some protection against freshwater exposure. Nevertheless, our models suggest that the decrease in salinity caused by fluvial discharge events poses a considerable abiotic challenge for *C. furcisetifer* and *D. pterophila* in the Ashburton River estuary, leading to diminished populations of these parasites.

The apparent sensitivity of *C. furcisetifer* and *D. pterophila* to changes in salinity highlights their potential as biological indicators. Ectoparasites, particularly monogeneans, can be useful biological indicators because they are typically in direct contact with the environment and susceptible to environmental stressors [72–76], can often be detected and removed non-invasively [77–79], and are highly host-specific [80–83]. Based on criteria proposed by Nachev & Sures [84] and Sures [85], *D. pterophila*, although having a narrow biogeographical range, appears to meet at least some of the conditions for being a suitable bioindicator: it is large enough to provide tissue for analyses and, like the other parasite species encountered in this study, can be easily observed *in situ* (Supplementary Fig. S1–S4), it is sessile and specific to *P. zijsron*, and it is sufficiently abundant. The health of coastal ecosystems in the Pilbara region is not well understood, and an effective bioindicator in this area could help with monitoring and mitigating potential threats for this important sawfish population. Additional work is required to characterise the physiology of *D. pterophila*, determine its distribution beyond the study area, and ascertain its susceptibility to particular pollutants [84,85].

4.2. Host-sex differences in ectoparasite infections

Intriguingly, infection intensities of *C. furcisetifer* and *D. pterophila* varied with host sex, and in opposing directions; female *P. zijsron* were host to more *C. furcisetifer*, whereas males were host to more *D. pterophila*. For both parasites, the discrepancy between host sexes only becomes apparent for juveniles over 2000 mm TL, and the opposing nature of this pattern is not easily explained. Host sex-related differences in parasite load can sometimes be explained by differences in host morphology, movement patterns, or behaviour [66,86], especially for parasites like copepods and monogeneans, which have direct transmission [80,87,88]. Some sexual dimorphism is apparent in *Pristis zijsron*; Lear et al. [22] found that the relative rostrum length of female *P. zijsron* was greater than males and Faria [89] reported that the height of the first dorsal fin on male *P. zijsron* was greater than females, and that the claspers on males become more elongated with growth and maturation, presenting additional body surface area for colonisation. However, additional work is required to determine whether these morphological differences could result in differences in intensity of infection between host sexes, and these results are based on few *P. zijsron* over 2000 mm TL.

4.3. Site specificity

Ectoparasites are typically specialised for attachment in particular areas of the host's body [50,90]. Distinct site-specificity is apparent for *C. furcisetifer* and *D. pterophila* on *P. zijsron*; 90% of *C. furcisetifer* were found on the head and rostrum, whereas *D. pterophila* were found almost exclusively posterior to the gills. Our evaluation of site-specificity revealed that sites with greater available surface area did not necessarily recruit greater numbers of parasites, as the pelvic fins are among the smallest sites. Intriguingly, the site-specificity for *C. furcisetifer* on the head of *P. zijsron* is consistent with observations by Morgan et al. [30] for this copepod on *P. pristis*, whereas the site-specificity for *D. pterophila* is different than for *Dermopristis paradoxa* Kearn, Whittington & Evans-Gowing, 2010 (emend.), on *P. pristis*, which instead attaches to the skin around the mouth [33]. This discrepant site-specificity between *D. pterophila* and *D. paradoxa* suggests differences in site preference between these species, or perhaps the role of an unexplained selective pressure, likely related to differences in morphology, behaviour or

ecology between *P. zijsron* and *P. pristis*. Site-specificity is common among ectoparasites [90], with segregation between coexisting ectoparasites often interpreted as an evolutionary consequence of interspecific competition, leading to ecological character displacement [90–94]. By dividing the host body surface into a number of discrete infection sites, our analysis suggests that the distributions of *C. furcisetifer* and *D. pterophila* on *P. zijsron* are influenced by intraspecific competition, due to the number of infection sites used by each species increasing with intraspecific intensity of infection.

Segregation between coexisting ectoparasite species may also arise through host and/or predator mediated interactions, such as grooming or cleaning [90,95]. Specificity for the head, rostrum and fins conceivably provides some protection against predation [96]. For example, parasitic copepods (including species of *Caligus*) form a large portion of the diet of echeneids [97–100], which were occasionally observed accompanying *P. zijsron* (Supplementary Fig. S5) in the study area, including sharksuckers, *Echeneis naucrates* Linnaeus, 1758, and remora, *Remora remora* (Linnaeus, 1758). Attempting to prey upon *C. furcisetifer* on the tooth-lined rostrum of a sawfish would not be without risk, as sawfishes use their rostrum to detect and capture prey [101].

The narrow site-specificity of *D. pterophila* on *P. zijsron* is perhaps most likely related to mating strategies [102,103]. Monogeneans are hermaphroditic, although for many species cross-fertilization is likely obligatory, and is thought to occur through the exchanging of spermatophore capsules for species of *Dermopristis* [34,104]. Rohde [102,103,105] provided several points of evidence for the 'mating hypothesis' as the cause of niche restriction in marine parasites, most of which are directly applicable to ectoparasites of *P. zijsron*, particularly *D. pterophila*, such as host-specificity, narrow habitat range (having not been found outside of the Pilbara region), and these flatworms being sessile on the host [20].

4.4. Sawfish ectoparasites on sympatric elasmobranchs

Metazoan parasites of elasmobranchs are poorly characterised, with hundreds of elasmobranch species yet to be thoroughly examined [50]. There are no previous reports of parasites infecting *R. palpebratus*, although this species has only recently been recognised as distinct from other *Rhynchobatus* species [106], from which several parasite taxa have been recorded [107,108]. In contrast, ectoparasites of *G. typus* have received moderate attention [29,34,109], although never in Western Australia. The occurrence of *C. furcisetifer* on *R. palpebratus* is not surprising, as this parasite has a relatively low host-specificity. However, it is intriguing that no *C. furcisetifer* were encountered on *G. typus*, a known host from eastern Australian waters [29]. Most *G. typus* surveyed in the Ashburton River and adjacent tidal creeks were small juveniles (432–669 mm) estimated to be YOY, based on age classes reported by White et al. [110], and have therefore had less time to accumulate parasites than mature *G. typus*, although we did find *C. furcisetifer* on the smallest sympatric *P. zijsron* (651 mm TL). Lastly, although *S. macrothela* has been found on numerous species of requiem sharks in Australian waters [21], it is unsurprising that this species was not found on *C. amblyrhynchoides*, *C. cautus* or *N. acutidens*, considering the low prevalence of leeches found on *P. zijsron* in the Ashburton River estuary (0–2%).

4.5. Conclusions

This study provides the foundation for numerous avenues of future study, including patterns in the distribution of parasite diversity, rates of speciation, diversification, and the local threat of extinction for several parasite taxa. Because the gene flow of *P. zijsron* in Australia is restricted at large spatial scales, with significant population structuring between assemblages [111], localised extinctions of *P. zijsron* could lead to the extinction of host-specific parasites such as *D. pterophila*, which is only known from *P. zijsron* in the study area. This is important to consider, not

just because of the potential loss of biodiversity, but because parasite species may serve as bioindicators of environmental quality and play key roles in the maintenance of ecosystem function.

Ethical approval

Handling and sampling of *P. zijsron* and bycatch species was conducted under Murdoch University Animal Ethics Approval: RW2397/11 and RW3191/19, Western Australian Government Department of Primary Industries and Regional Development fisheries exemption no. 3378 and 3553, Department of Fisheries Regulation 178 (SPA 11–11), and Department of Environment and Conservation Permit SF007889.

CRediT authorship contribution statement

Jack Ingelbrecht: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Karissa O. Lear:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Storm B. Martin:** Writing – review & editing, Methodology, Investigation. **Alan J. Lymbery:** Writing – review & editing, Investigation, Formal analysis, Conceptualization. **Bradley M. Norman:** Writing – review & editing, Conceptualization. **Geoffrey A. Boxshall:** Writing – review & editing. **David L. Morgan:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization.

Declaration of competing interest

The authors declare there are no competing interests associated with this research.

Data availability

The data used in this study are available from the corresponding author upon reasonable request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.parint.2024.102900.

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