Syst Parasitol (2024) 101:20
https://doi.org/10.1007/s11230-023-10145-w

Marine fish parasites in the Cat Ba Archipelago, Vietnam: the results of 2010-2023 field surveys

Hoang-Ha Thi Nguyen · Ha Van Nguyen · Hoang Van Hien · Nguyen Ngoc Chinh · Vinh Thi Thanh Truong · Van Van Kim · Truong Dinh Hoai · Phuc Pham Duc · Stephen E. Greiman · Hung Manh Nguyen

Received: 27 August 2023 / Accepted: 19 December 2023

Abstract Between 2010 and 2023, a longitudinal study was undertaken to uncover the diversity of the parasite fauna of marine fishes in the Cat Ba Archipelago, a world biosphere reserve, in Vietnam. A total of 1,042 specimens representing 80 different fish species were collected and examined. Of these, 68 fish species, represented by 994 specimens (95.39%), were infected with parasites. A total of 162 parasitic species were discovered, including 54 trematodes, 37 monogeneans, 27 crustaceans, 15 myxozoans, 10 acanthocephalans, 10 nematodes, 7 cestodes, and 2 hirudineans. Over the course of the survey, twenty new species were described, including 7 acanthocephalans and 13 trematodes. Additionally, twenty species were recorded for the first time from the Cat Ba Archipelago and twenty-two species had new host records reported. The prevalence and mean intensity of parasite infection were found to be unaffected by season. These data on the parasitic fauna of Cat Ba Archipelago not only expand our knowledge of the diversity of Vietnam, but also provide strong baseline data for measuring future change resulting from environmental perturbations.

H.-H. T. Nguyen · H. Van Nguyen · H. Van Hien · N. N. Chinh · H. M. Nguyen (✉)
Institute of Ecology and Biological Resources, Graduate University of Science and Technology, Vietnam Academy of Science and Technology, Hanoi, Vietnam
e-mail: hung_iebr@yahoo.com

V. T. T. Truong
Scholl of Agriculture and Natural Resources, Vinh University, Vinh City, Vietnam

V. Van Kim · T. D. Hoai
Faculty of Fisheries, Vietnam National University of Agriculture, Hanoi, Vietnam

P. P. Duc
Center for Public Health and Ecosystem Research, Hanoi University of Public Health, Hanoi, Vietnam

P. P. Duc
Institute of Environmental Health and Sustainable Development, Hanoi, Vietnam

S. E. Greiman
Georgia Southern University, Statesboro, Georgia, USA

Introduction

Cat Ba Archipelago, located along the southeastern edge of Lan Ha Bay in Northern Vietnam, comprises 367 islands spread across an area of nearly 300 km^2 (Thanh et al., 2015). The largest island, Cat Ba Island, covers an area of 260 km^2. Situated at the heart of the island is Cat Ba National Park, encompassing 109 km^2 of land area and an additional 52 km^2 of inshore waters and mangrove-covered tidal zones. The park was recognized by UNESCO in 2004 as a world network biosphere reserve. Together with Halong Bay, Cat Ba Archipelago forms spectacular karst landscapes, characterized by limestone cones and towers submerged within the sea (Thung et al. 2019).

Published online: 14 February 2024

Within the archipelago, there are seven distinct ecosystems present on the limestone islands, namely tropical rainforest, cave, mangrove, tidal, salt lake, coral, and soft bottom systems. This ecological diversity contributes to the rich biodiversity found within the region. A total of 4,622 species have been recorded within the Cat Ba Archipelago and adjacent areas, including 11 freshwater and 361 marine fishes (Thung et al., 2019). However, Thung et al. (2019) did not document the parasite species diversity on and within these fishes, although several publications of endo- and ecto-parasites are available, e.g. Amin and Ha (2011), Garasev et al. (2011a, b), Amin et al. (2011a, b, c, 2018), Dmitrieva et al. (2013, 2018), Kazachenko et al. (2014a, b, 2017), Besprozvannykh et al. (2015, 2016, 2017, 2018), Atopkin et al. (2017a, b). Therefore, within this paper, we provide a more robust sampling of the ecto- and endo- parasite diversity of marine fishes within the Cat Ba Archipelago conduncted over 13 years (2010-2023).

Materials and methods

Fish sampling

Fish samples were collected throughout the Cat Ba Archipelago on nine occasions, seven times in the dry season (March-April) and twice in the rainy season (September-October) between 2010 and 2023. Fish samples were purchased alive from the local fishery, euthanized immediately with benxocaine (100 mg/l), placed individually in polythene bags, kept in an ice box, and carried fresh to the laboratory. Each fish was identified to species according to Huong (2001), Phung (2001), Thi (2008), Allen (2009) and also by data on FishBase (https://www.fishbase.se/).

Sample collecting

The skin, fins, scales, eyes, mouth, oral cavity, nostril, intestine, stomach, kidney, gall bladder, and muscle of fish hosts were thoroughly examined for the presence of parasites under an Olympus SZ61 stereomicrosope. Additionally, smears obtained from cysts on various organs, e.g. bile of gall bladder, contents of the urinary bladder, and muscle tissues, were examined on an Olympus CH40 microscope to detect myxozoa and protistan parasites. Parasites were collected, fixed, and preserved following standard procedures described by Buchmann (2007).

Parasite identification

For morphological identification, permanent mounts were prepared following standard methods for trematodes, monogeneans, cestodes, acanthocephanlans, and nematodes (Kritsky et al., 1978; Buchmann, 2007; Hoffman, 1999). Crustaceans (copepods, isopods) were cleared in lactic acid before dehydration and microscopical examination (Kabata, 1979). Hirudinea were observed with a dissecting microscope and internal anatomy was observed through histological sections prepared following the methods of Sawyer et al. (1975). Smear preparations for myxozoa and protistan parasites were conducted according to Lom & Arthur (1989). To supplement light microscope examination, the external morphology of acanthocephalans and nematodes were also imaged on a scanning electron microsope (FEI X L30 ESEMFEG) (Amin & Ha, 2011; Hien et al., 2021).

The taxonomic identification of some parasites was also based on the molecular and phylogenetic analysis. DNA from parasite specimens were extracted using a Qiagen™ (Valencia, California, USA) DNeasy® Tissue Kit, or Hot-SHOT technique (Truett et al., 2000); and target genes were amplified using appropriate primers. The COI, 18S, ITS1-5.8S-ITS2, and 28S genes of acanthocephalans were amplified using the following primers LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3') (forward) and HC02198 (5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3' (reverse) (Folmer et al., 1994) for the COI gene; Worm A (5′-GCG AAT GGC TCA TTA AAT CAG-3′) and 1270R (5′-CCG TCA ATT CCT TTA AGT-3′) (Littlewood & Olson, 2001) for the 18S gene; BD1 (5′-GTC GTA ACA AGG TTT CCG TA-3′) and BD2 (5′-TAT GCT TAA ATT CAG CGG GT-3′) (Galazzo et al., 2002) for the ITS1-5.8S-ITS2 region; L300F (5′-CAA GTA CCG TGA GGG AAA GTT G-3′) and ECD2 (5′-CCT TGG TCC GTG TTT CAA GAC GGG-3′) (Littlewood et al., 2000) for the 28S gene. For trematodes, various genes, e.g. 18S rDNA, 28S rDNA, and ITS1-5.8S-ITS2 (Atopkin et al. 2017a,b; Besprozvannykh et al. 2015, 2016, 2017, 2018) were amplified by the primer sets 18S-E (5'-CCG AAT TCG TCG ACA ACC TGG TTG ATC CTG CCA GT-3'), 18S-F (5'-CCA GCT TGA TCC

Table 1 Parasite group prevalence from Fishes sampled from Cat Ba Archipelago.

	Fish species	Number examined	Parasite group (No. infection/no. parasites)							
			Acantho-cephalan	Ces-todes	Tremato-des	Mono-genean	Nema-toda	Hiru-dinea	Crusta-cean	Myxo-zoa
I	ACANTHURIFORMES									
1	**Leiognathidae Gill**									
1	*Aurigequula fasciata* (Lacépède)	5	4/7				1/1			
2	*Equulites rivulatus* (Temminck & Schlegel)	3							1/1	
3	*Photolateralis stercorarius* (Evermann & Seale)	1								
2	**Siganidae Richardson**									
4	*Siganus fuscescens* (Houttuyn)	64			13/111	53/520	11/58		2/2	
II	ANGUILLIFORMES									
3	**Anguillidae Rafinesque**									
5	*Anguilla marmorata* Quoy & Gaimard	5								
4	**Muraenesocidae Kaup**									
6	*Muraenesox cinereus* (Forsskål)	38		2/7	9/45		9/163		12/82	
III	AULOPIFORMES									
5	**Synodontidae Gill**									
7	*Saurida tumbil* (Bloch)	10			1/3					
IV	BELONIFORMES									
6	**Belonidae Bonaparte**									
8	*Ablennes hians* (Valenciennes)	20								
9	*Strongylura leiura* (Bleeker)	1				1/2				
10	*Strongylura strongylura* (van Hasselt)	8	3/5		3/19	7/65			3/9	
11	*Xenentodon cancila* (Hamilton)	4				1/5				
7	**Hemiramphidae Gill**									
12	*Hemiramphus far* (Forsskål)	5			4/9	5/35				1

Table 1 (continued)

	Fish species	Number examined	Parasite group (No. infection/no. parasites)							
			Acantho-cephalan	Ces-todes	Tremato-des	Mono-genean	Nema-toda	Hiru-dinea	Crusta-cean	Myxo-zoa
13	*Hemiramphus marginatus* (Forsskål)	15			2/3	10/51				3
14	*Hyporhamphus quoyi* (Valenciennes)	28	3/5			7/48				
15	*Rhynchorhamphus georgii* (Valenciennes)	61			2/3	11/22				
V	CARANGARIA *incertae sedis*									
8	**Sphyraenidae Rafinesque**									
16	*Sphyraena obtusata* Cuvier	10			1/2	2/2			2/5	
9	**Polynemidae Rafinesque**									
17	*Leptomelanosoma indicum* (Shaw)	2	1/4		1/35				1/3	
VI	CENTRARCHIFORMES									
10	**Terapontidae Richardson**									
18	*Terapon jarbua* (Forsskål)	16				2/26			1/3	
11	**Tetraodontidae Richardson**									
19	*Terapon theraps* Cuvier	2			1/3	1/1				
VII	CLUPEIFORMES									
12	**Dorosomatidae Gill**									
20	*Anodontostoma chacunda* (Hamilton)	3			2/10					
21	*Clupanodon* sp.	5								
22	*Tenualosa thibaudeaui* (Durand)	10				3/38				
13	**Engraulidae Gill**									
23	*Coilia rebentischii* Bleeker	10				4/5				
24	*Thryssa dussumieri* (Valenciennes)	17				5/13			5/15	
14	**Pristigasteridae Bleeker**									

Table 1 (continued)

	Fish species	Number examined	Parasite group (No. infection/no. parasites)							
			Acantho-cephalan	Ces-todes	Tremato-des	Mono-genean	Nema-toda	Hiru-dinea	Crusta-cean	Myxo-zoa
25	*Ilisha elongata* (Anonymous [Bennett])	2			1/25		1/1			
26	*Ilisha megaloptera* (Swainson)	5				4/41				
VIII	EUPERCARIA *incertae sedis*									
15	**Gerreidae Bleeker**									
27	*Gerres filamentosus* Cuvier	8				2/50			1/2	
28	*Gerres oyena* (Forsskål)	5								
16	**Malacanthidae Poey**									
29	*Branchiostegus japonicus* (Houttuyn)	5								
17	**Nemipteridae Regan**									
30	*Nemipterus japonicus* (Bloch)	15		1/5	1/1	9/309	2/4			13
18	**Sciaenidae Cuvier**									
31	*Argyrosomus japonicus* (Temminck & Schlegel)	12		2/7	3/4	11/52	4/24		4/13	
32	*Nibea albiflora* (Richardson)	8	3/54	1/1	5/26	5/42	2/8		1/1	
33	*Nibea soldado* (Lacépède)	1								
34	*Johnius belangerii* (Cuvier)	15	2/7		1/1				4/5	
35	*Johnius carouna* (Cuvier)	5		1/5	3/7	3/4	3/9			
36	*Otolithes ruber* (Bloch & Schneider)	5	3/5						1/2	
19	**Sillaginidae Richardson**									
37	*Sillago sihama* (Forsskål)	14			8/53	13/411	1/1			
20	**Sparidae Rafinesque**									
38	*Acanthopagrus latus* (Houttuyn)	3			3/31				1/3	
IX	GONORYNCHIFORMES									

Table 1 (continued)

	Fish species	Number examined	Parasite group (No. infection/no. parasites)							
			Acantho-cephalan	Ces-todes	Tremato-des	Mono-genean	Nema-toda	Hiru-dinea	Crusta-cean	Myxo-zoa
21	**Chanidae Günther**									
39	*Chanos chanos* (Forsskål)	1								
X	HOLOCENTRIFORMES									
22	**Holocentridae Bonaparte**									
40	*Sargocentron rubrum* (Forsskål)	20			4/4	12/153				
XI	MUGILIFORMES									
23	**Mugilidae Jarocki**									
41	*Crenimugil heterocheilos* (Bleeker)	10	1/3		3/3	4/157				
42	*Crenimugil seheli* (Fabricius)	41			26/473	1/4				
43	*Ellochelon vaigiensis* (Quoy & Gaimard)	3	1/9		1/52	2/38				
44	*Liza longimanus* (Günther)	3	1/1		2/53					
45	*Mugil cephalus* Linnaeus	35	2/2		11/151	10/370		5/13	7/10	
46	*Osteomugil cunnesius* (Valenciennes)	18		1/1	5/65	1/50	1/1		1/4	5
47	*Osteomugil engeli* (Bleeker)	95	1/2		49/592	9/80			1/1	15
48	*Osteomugil speigleri* (Bleeker)	36			1/1					
49	*Planiliza affinis* (Günther)	1				1/1				
50	*Planiliza haematocheilus* (Temminck & Schlegel)	3	1/1		3/11					
51	*Planiliza melinoptera* (Valenciennes)	83			11/35	17/37		1/2		
52	*Planiliza planiceps* (Valenciennes)	3			2/138	1/1				
53	*Planiliza subviridis* (Valenciennes)	31	10/20		22/240	10/60				13
XII	MULLIFORMES									
24	**Mullidae Rafinesque**									

Table 1 (continued)

	Fish species	Number examined	Parasite group (No. infection/no. parasites)							
			Acantho-cephalan	Ces-todes	Tremato-des	Mono-genean	Nema-toda	Hiru-dinea	Crusta-cean	Myxo-zoa
54	*Upeneus tragula* Richardson	10				5/95			5/13	
XIII	MYLIOBATIFORMES									
25	**Dasyatidae Jordan & Gilbert**									
55	*Hemitrygon akajei* (Müller & Henle)	1								
XIV	SCOMBRIFORMES									
26	**Ariommatidae Haedrich**									
56	*Ariomma indica* (Day)	10		5/14	4/12		1/1			
27	**Scombridae Rafinesque**									
57	*Scomberomorus commerson* (Lacépède)	12			1/1	11/91				4
28	**Trichiuridae Rafinesque**									
58	*Trichiurus lepturus* Linnaeus	20		3/30	2/3	8/11	6/21		4/4	
XV	SILURIFORMES									
29	**Plotosidae Bleeker**									
59	*Plotosus lineatus* (Thunberg)	10	10/350				1/1		1/2	
XVI	PERCIFORMES									
30	**Carangidae Rafinesque**									
60	*Alepes djedaba* (Forsskål)	15			10/134	6/69				
61	*Atropus atropos* (Bloch & Schneider)	5			1/5					
62	*Atule mate* (Cuvier)	10			7/45					
63	*Decapterus maruadsi* (Temminck & Schlegel)	5							1/1	
64	*Decapterus russelli* (Rüppell)	10				2/2			1/5	
65	*Megalaspis cordyla* (Linnaeus)	5				5/65				2

Table 1 (continued)

	Fish species	Number examined	Parasite group (No. infection/no. parasites)							
			Acantho-cephalan	Ces-todes	Tremato-des	Mono-genean	Nema-toda	Hiru-dinea	Crusta-cean	Myxo-zoa
66	*Scomberoides commersonnianus* Lacépède	9		1/1	5/76	4/23	1/1		2/2	
67	*Selar crumenophthalmus* (Bloch)	5			3/24	2/2				
68	*Selaroides leptolepis* (Cuvier)	3			1/1		2/6			
69	*Parastromateus niger* (Bloch)	5			3/6					
31	**Platycephalidae Swainson**									
70	*Platycephalus indicus* (Linnaeus)	23	1/5	1/1	5/24	4/82	1/2		1/4	7
32	**Scatophagidae Gill**									
71	*Scatophagus argus* (Linnaeus)	7							1/2	
33	**Serranidae Swainson**									
72	*Diploprion bifasciatum* Cuvier	12							6/12	
73	*Epinephelus bleekeri* (Vaillant)	1								
74	*Epinephelus sexfasciatus* (Valenciennes)	5			1/2	5/59				
75	*Epinephelus trophis* Randall & Allen	2								
34	**Scorpaenidae Risso**									
76	*Pterois russelii* Bennett	1								
XVII	PLEURONECTIFORMES									
35	**Cynoglossidae Jordan**									
77	*Cynoglossus bilineatus* (Lacépède)	9							1/1	
XVIII	TETRAODONTI-FORMES									
37	**Monacanthidae Nardo**									

Table 1 (continued)

	Fish species	Number examined	Parasite group (No. infection/no. parasites)							
			Acantho-cephalan	Ces-todes	Tremato-des	Mono-genean	Nema-toda	Hiru-dinea	Crusta-cean	Myxo-zoa
78	*Aluterus monoceros* (Linnaeus)	1			1/1					
79	*Monacanthus chinensis* (Osbeck)	4			1/1				4/14	
38	**Tetraodontidae Bonaparte**									
80	*Lagocephalus lunaris* (Bloch & Schneider)	5		1/1	2/60	1/1			1/1	
	Total	1,042	47/480	19/73	251/2,604	280/3,193	47/302	6/15	76/222	63/-

TTC TGC AGG TTC ACC TAC-3') for the 18S gene (Littlewood & Olson, 2001), DIG12 (5'-AAG CAT ATC ACT AAG CGG-3') and 1500R (5'-GCT ATC CTG AGG GAA ACT TCG-3') for the 28S gene (Tkach et al., 2003), and ITSF (5′-CGC CCG TCG CTA CTA CCG ATT G-3′) (Andres et al., 2014) and S4R (5′-TAT GCT TAA ATT CAG CGG GT-3′) for the ITS1-5.8S-ITS2 fragment (Besprozvannykh et al., 2019). The nucleotide sequences were assembled manually and aligned by specific solfware. Reconstruction of the phylogenetic relationship was performed using data of other closely related parasitic species available in the GenBank database.

Statistical analysis

Data were entered into an Excel worksheet (Microsoft Corporation, Redmond, Washington) and analyzed using STATA/IC 12 (Stata Corp LP, College Station, TX). Parasites count data from fish samples were transformed to binomial data. Fish with infection of any parasite species was coded to "1" and uninfected fish was coded to "0". Parasite infections of fishes were analyzed using logistic regressions, with fish species, fish family, fish order, and season as predictors after adjusting for groups of fish collected from a single fish haul and collection times. Differences with P-values below 0.05 were considered significant.

Results

Fish host diversity and parasite prevelaence

In total, 1,042 marine fish specimens, representing 80 species of 38 genera and 17 orders were collected and examined (Table 1). Perciformes was the most diverse order sampled with 16 species, followed closely by Mugiliformes with 13 species; the remaining 15 orders were represented by one to eight species each (Table 1). Mugilidae and Carangidae were the most diverse families, comprising 13 and 10 species, respectively. The number of species present in other families ranged from 1 to 6. Five species including 3 mugilids *Osteomugil engeli* (Bleeker), *Planiliza melinoptera* (Valenciennes), *Crenimugil seheli* (Fabricius), 1 siganid *Siganus fuscescens* (Houttuyn), and 1 hemiramphid *Rhynchorhamphus georgii*

Table 2 Host and Parasite data for Cat Ba Archipelago

Parasite species	Fish host	Infection site	No. infected/No. examined	Intensity of infection: mean (range)	GenBank numbers of submitted sequences	Specimen stored
ACANTHOCEPHALA						
ECHINORHYNCHIDA SOUTHWELL ET MACFIE, 1925						
Arhythmacanthidae Yamaguti, 1935						
***Heterosentis* van Cleave, 1931**						
**Heterosentis holospinus* Amin, Heckmann & Nguyen, 2011	*Plotosus lineatus*	intestine	10/10	35 (3-60)	MN715352- MN715355	University of Nebraska's State Museum's Harold W. Manter Laboratory, USA (HWML): nos. 49254-49255; Department of Parasitology, Insitute of Ecology and Biological Resources, Vietnam Academy of Science and Technology (IEBR)
Isthmosacanthidae Smales, 2012						
***Serrasentis* Van Cleave, 1923**						
****Serrasentis sagittifer* (Linton, 1889) Linton, 1932	*Platycephalus indicus*	intestine	1/23	5	n.s.	IEBR
Rhadinorhynchidae Lühe, 1912						
***Micracanthorhynchina* Strand, 1936**						
**Micracanthorhynchina kuwaitensis* Amin & Sey, 1996	*Hyporhamphus quoyi*	intestine	3/28	1.7 (1-2)	n.s.	IEBR
Family Transvenidae Pichelin & Cribb, 2001						
***Pararhadinorhynchus* Johnston & Edmonds, 1947**						
**Pararhadinorhynchus magnus* Nguyen, Amin, Ha & Heckmann, 2018	*Mugil cephalus*	intestine	2/35	1	MN820556;MN820614; MN472865; MN472866; MN395026; MN395027	HWML no. 139410-139411; IEBR
NEOECHINORHYNCHIDA WARD, 1917						
Neoechinorhynchidae Ward, 1917						
***Neoechinorhynchus* Hamann in Stiles & Hassall, 1905**						
**Neoechinorhynchus* (*Neoechinorhynchus*) *ascus* Amin, Ha & Ha, 2011	*Osteomugil engeli*	intestine	1/95	2	n.s.	HWML nos. 49218-49219; IEBR
**Neoechinorhynchus* (*Neoechinorhynchus*) *dimorphospinus* Amin & Sey, 1996	*Planiliza haematocheilus*	intestine	1/3	1	n.s.	IEBR
	Planiliza subviridis	intestine	10/31	2 (1-4)	MK510080	HWML; IEBR
Neoechinorhynchus (*Neoechinorhynchus*) *johnii* Yamaguti, 1939	*Johnius belangerii*	intestine	2/15	3.5 (2-5)	MK260005-MK260008	HWML nos. 139459, 139460, 139465, 139466, 139468; IEBR
	Otolithes ruber	intestine	3/5	1.7 (1-2)		HWML nos. 139462, 139467; IEBR

Table 2 (continued)

Parasite species	Fish host	Infection site	No. infected/No. examined	Intensity of infection: mean (range)	GenBank numbers of submitted sequences	Specimen stored
**Neoechinorhynchus* (*Neoechinorhynchus*) *longinucleatus* Amin, Nguyen & Ha, 2011a, 2011b, 2011c	*Aurigequula fasciata*	intestine	4/5	2.3 (1-3)	n.s.	IEBR
	Crenimugil heterocheilos	intestine	1/10	3		
	Ellochelon vaigiensis	intestine	1/3	9		
	Liza longimanus	intestine	1/3	1		
	Strongylura strongylura	intestine	3/5	1.7 (1-3)		HWML Collection no. 49216-49217: IEBR
**Neoechinorhynchus* (*Neoechinorhynchus*) *manubriensis* Amin, Nguyen & Ha, 2011a, 2011b, 2011c	*Nibea albiflora*	intestine	3/8	18 (3-29)	n.s.	HWML no. 49211; IEBR
****Neoechinorhynchus indicus* Gudivada, Chikkam & Vankara, 2010	*Leptomelanosoma indicum*	intestine	1/2	4	n.s.	IEBR
CESTODA						
BOTHRIOCEPHALIDEA KUCHTA, SCHOLZ, BRABEC & BRAY, 2008						
Bothriocephalidae Blanchard, 1849						
***Bothriocephalus* Rudolphi, 1808**						
†*Bothriocephalus* sp.	*Trichiurus lepturus*	intestine	3/20	10 (8-12)	n.s.	IEBR
***Taphrobothrium* Lühe, 1899**						
Taphrobothrium japonense Lühe, 1899	*Muraenesox cinereus*	intestine	2/38	3.5 (2-5)	n.s.	IEBR
TETRAPHYLLIDEA CARUS, 1863						
†Tetraphyllidea fam. gen. sp.	*Argyrosomus japonicus*	intestine	2/7	3.5 (2-5)	n.s.	IEBR
	Johnius carouna	intestine	1/5	5		
	Lagocephalus lunaris	intestine	1/5	1		
	Nemipterus japonicus	intestine	1/15	5		
	Nibea albiflora	intestine	1/8	1		
TRYPANORHYNCHA DIESING, 1863						
Lacistorhynchidae Guiart, 1937						
***Pseudogrillotia* Dollfus, 1969**						
Pseudogrillotia perelica (Shuler, 1938) Palm, 2004	*Osteomugil cunnesius*	intestine	1/18	1	n.s.	IEBR
Otobothriidae Dollfus, 1942						
***Poecilancistrium* Dollfus, 1929**						
†*Poecilancistrium* sp. Plerocercoid	*Ariomma indica*	intestine	5/10	2.8 (1-10)	n.s.	IEBR
***Proemotobothrium* Beveridge & Campbell, 2001**						
Proemotobothrium linstowi (Southwell, 1912) Beveridge & Campbell, 2001	*Platycephalus indicus*	intestine	1/23	1	n.s.	IEBR
Tentaculariidae Poche, 1926						
***Tentacularia* Bosc, 1797**						
Tentacularia coryphaenae Bosc, 1802	*Scomberoides commersonnianus*	intestine	1/9	1	n.s.	IEBR

Table 2 (continued)

Parasite species	Fish host	Infection site	No. infected/No. examined	Intensity of infection: mean (range)	GenBank numbers of submitted sequences	Specimen stored
TREMATODA						
PLAGIORCHIIDA LA RUE, 1957						
Acanthocolpidae Lühe, 1906						
***Pleorchis* Railliet, 1896**						
Pleorchis sciaenae Yamaguti, 1938	*Acanthopagrus latus*	intestine	3/3	4.3 (3-4)	n.s.	IEBR
***Stephanostomum* Looss, 1899**						
Stephanostomum bicoronatum (Stossich, 1883) Fuhrmann, 1928	*Argyrosomus japonicus*	intestine	3/12	1.3 (1-2)	n.s.	IEBR
	Johnius carouna	intestine	3/5	2.3 (1-3)		
Stephanostomum ditrematis (Yamaguti, 1939) Manter, 1947	*Scomberoides commersonnianus*	intestine	1/9	50	n.s.	IEBR
Bivesiculidae Yamaguti, 1934						
***Paucivitellosus* Coil, Reid & Kuntz, 1965**						
**Paucivitellosus vietnamensis* Atopkin, Besprozvannykh, Ngo, Van Ha, Van Tang, Ermolenko & Beloded, 2016	*Crenimugil seheli*	intestine	1/41	14	LN865005- LN865006; LN864998- LN865000; LN865003- LN865004	Zoological Museum, Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of Russian Academy of Sciences (FSCEAT): nos. 61-64-Tr; IEBR
	Osteomugil engeli	intestine	6/95	4.2 (2-9)		
	Planiliza melinoptera	intestine	6/83	11.3 (3-20)	n.s.	IEBR
	Planiliza planiceps	intestine	2/3	69 (1-137)	n.s.	IEBR
	Planiliza subviridis	intestine	11/79	3.2 (1-7)	LN865001-LN865002	FSCEAT no. 60-Tr; IEBR
***Treptodemoides* Shen, 1995**						
Treptodemoides fukenensis (Liu, 1995) Cribb, 2002	*Rhynchorhamphus georgii*	intestine	2/61	1.5 (1-2)	n.s.	IEBR
Bucephalidae Poche, 1907						
***Bucephalus* von Baer, 1827**						
Bucephalus fragilis Velasquez, 1959	*Scomberoides commersonnianus*	intestine	2/9	6 (4-8)	n.s.	IEBR
Bucephalus margaritae Ozaki & Ishibashi, 1934	*Atropus atropos*	intestine	1/5	5	n.s.	IEBR
	Atule mate	intestine	2/10	2.5 (2-3)		
	Selar crumenophthalmus	intestine	1/5	18		
Bucephalus sp.1	*Sphyraena obtusata*	intestine	1/10	2	n.s.	IEBR
Bucephalus sp.2	*Anodontostoma chacunda*	intestine	2/3	5 (2-8)	n.s.	IEBR
***Prosorhynchus* Odhner, 1905**						
Prosorhynchus epinepheli Yamaguti, 1939	*Epinephelus sexfasciatus*	intestine	1/5	2	n.s.	IEBR
Cryptogonimidae Ward, 1917						
***Adlardia* Miller, Bray, Goiran, Justine & Cribb, 2009**						
Adlardia elongata (Gu & Shen, 1979) Miller, Bray, Goiran, Justine & Cribb, 2009	*Nemipterus japonicus*	intestine	1/15	1	n.s.	IEBR

Table 2 (continued)

Parasite species	Fish host	Infection site	No. infected/No. examined	Intensity of infection: mean (range)	GenBank numbers of submitted sequences	Specimen stored
Fellodistomidae Nicoll, 1909						
***Gymnotergestia* Nahhas & Cable, 1964**						
**Gymnotergestia strongyluri* Atopkin, Besprozvannykh, Ha, Nguyen & Nguyen, 2022	*Strongylura strongylura*	Intestine	1/8	2	OK636408- OK636409	FSCEAT nos. 199-203-Tr; IEBR
***Lintonium* Stunkard & Nigrelli, 1930**						
Lintonium vibex (Linton, 1900) Stunkard & Nigrelli, 1930	*Aluterus monoceros*	Intestine	1/1	1	n.s.	IEBR
***Monascus* Looss, 1907**						
Monascus filiformis (Rudophi, 1819) Looss, 1907	*Ariomma indicum*	Intestine	4/10	3 (1-8)	n.s.	IEBR
Gyliauchenidae Fukui, 1929						
***Gyliauchen* Nicoll, 1915**						
Gyliauchen oligoglandulosus Gu & Shen, 1979	*Siganus fuscescens*	Intestine	11/64	4.7 (1-9)	n.s.	IEBR
Haploporidae Nicoll, 1914						
***Parahaploporus* Atopkin, Besprozvannykh, Ha, Nguyen & Nguyen, 2019**						
**Parahaploporus elegantus* Atopkin, Besprozvannykh, Ha, Nguyen & Nguyen, 2019	*Osteomugil cunnesius*	Intestine	2/18	24 (6-42)	MN639712- MN639721	FSCEAT nos. 143-147-Tr; IEBR
***Parasaccocoelium* Zhukov, 1971**						
Parasaccocoelium mugili Zhukov, 1971	*Mugil cephalus*	Intestine	5/35	17.4 (2-35)	n.s.	IEBR
***Paraunisaccoides* Martin, 1973**						
**Paraunisaccoides elegans* Atopkin, Besprozvannykh, Beloded, Ha, Nguyen & Nguyen, 2022	*Planiliza subviridis*	Intestine	3/31	6.2 (1-12)	KY501639- KY501644	FSCEAT nos. 182-187-Tr; IEBR
***Pseudohaploporus* Atopkin, Besprozvannykh, Ha, Nguyen, Nguyen & Chalenko, 2018**						
**Pseudohaploporus planilizum* Atopkin, Besprozvannykh, Ha, Nguyen, Nguyen & Chalenko, 2018	*Planiliza subviridis*	intestine	3/31	16.7 (7-29)	MF774417–MF774419; MF774433–MF774435	FSCEAT nos. 128-137-Tr; IEBR
**Pseudohaploporus pusitestis* Atopkin, Besprozvannykh, Ha, Nguyen & Nguyen, 2019	*Crenimugil seheli*	intestine	1/41	5	MH986037; MH986038; MF774430; MF774432	FSCEAT nos. 138-142-Tr; IEBR
**Pseudohaploporus vietnamensis* Atopkin, Besprozvannykh, Ha, Nguyen, Nguyen & Chalenko, 2018	*Crenimugil seheli*	intestine	2/41	15 (14-16)	MF774422; MF774431	FSCEAT nos. 118-127-Tr: IEBR
	Osteomugil engeli	intestine	7/95	12.6 (5-24)	MF774420-MF774421; MF774423-MF774426; MF774427-MF774429; MF774436-MF774440	
	Osteomugil speigleri	intestine	1/36	1	n.s.	

Table 2 (continued)

Parasite species	Fish host	Infection site	No. infected/No. examined	Intensity of infection: mean (range)	GenBank numbers of submitted sequences	Specimen stored
***Skrjabinolecithum* Belous, 1954**						
Skrjabinolecithum spasskii Belous, 1954	*Mugil cephalus*	intestine	6/35	10.7 (1-28)	HG530203-HG530209; HG530224-HG530230	FSCEAT no. 62-Tr; IEBR
	Planiliza haematocheilus	intestine	3/3	3.7 (1-7)	n.s.	IEBR
***Unisaccus* Martin, 1973**						
**Unisaccus halongi* Atopkin, Besprozvannykh, Beloded, Ha, Nguyen & Nguyen, 2022	*Crenimugil seheli*	intestine	5/41	5.4 (1-17)	OK644190-OK644198	FSCEAT nos. 188-193-Tr; IEBR
**Unisaccus tonkini* Besprozvannykh, Atopkin, Ngo, Ha, Tang & Beloded, 2017	*Crenimugil seheli*	intestine	7/41	15 (7-28)	MF176835-MF176844	FSCEAT nos. 94-103-Tr; IEBR
	Osteomugil cunnesius	intestine	3/18	5.7 (1-12)	n.s.	
Haplosplanchnidae Poche, 1926						
***Haplosplanchnus* Looss, 1902**						
Haplosplanchnus pachysoma (Eysenhardt, 1829) Looss, 1902	*Osteomugil engeli*	intestine	5/95	10 (8-18)	LK932143–LK932146; LK932149–LK932152	FSCEAT; IEBR
***Provitellotrema* Pan, 1984**						
Provitellotrema crenimugilis Pan, 1984	*Crenimugil heterocheilos*	intestine	3/10	1	LK932147–LK932148; LK932153–LK932154	FSCEAT; IEBR
***Pseudohaplosplanchnus* Atopkin, Besprozvannykh, Ha, Nguyen & Nguyen, 2020**						
**Pseudohaplosplanchnus catbaensis* Atopkin, Besprozvannykh, Ha, Nguyen & Nguyen, 2020	*Crenimugil seheli*	intestine	6/41	43 (2-181)	MT298954-MT298957; MT298959-MT298962	FSCEAT nos. 157-161-Tr; IEBR
Hemiuridae Looss, 1899						
***Aphanurus* Looss, 1907**						
Aphanurus mugilus Tang, 1981	*Osteomugil engeli*	intestine	9/95	12.2 (1-41)	LT607804– LT607809	FSCEAT; IEBR
***Dinurus* Looss, 1907**						
Dinurus selari Parukhin, 1966	*Atule mate*	intestine	5/10	8 (4-15)	n.s.	IEBR
***Ectenurus* Looss, 1907**						
Ectenurus theraponae Oshmarin, 1965	*Terapon theraps*	intestine	1/2	3	n.s.	IEBR
Ectenurus trachuri (Yamaguti, 1934) Yamaguti, 1970	*Selar crumenophthalmus*	intestine	1/5	4	n.s.	IEBR
***Hemiurus* Rudolphi, 1809**						
Hemiurus arelisci Yamaguti, 1938	*Scomberoides commersonnianus*	intestine	2/9	7 (3-11)	n.s.	IEBR
	Scomberomorus commerson	intestine	1/12	1		
***Lecithochirium* Lühe, 1901**						
Lecithochirium alectis Yamaguti, 1970	*Johnius belengerii*	intestine	1/15	1	n.s.	IEBR
	Nibea albiflora	intestine	5/8	5.2 (1-18)		

Table 2 (continued)

Parasite species	Fish host	Infection site	No. infected/No. examined	Intensity of infection: mean (range)	GenBank numbers of submitted sequences	Specimen stored
Lecithochirium holocentri Yamaguti, 1970	*Sargocentron rubrum*	intestine	4/20	1	n.s.	IEBR
Lecithochirium polynemi Chauhan, 1945	*Leptomelanosoma indicum*	intestine	1/2	35	n.s.	IEBR
***Lecithocladium* Lühe, 1901**						
Lecithocladium excisiforme Cohn, 1902	*Alepes djedaba*	intestine	10/15	13.4 (2-20)	n.s.	IEBR
	Selaroides leptolepis	intestine	1/3	1		
Lecithocladium harpodontis Srivastava, 1937	*Ilisha elongata*	intestine	1/2	25	n.s.	IEBR
***Merlucciotrema* Yamaguti, 1971**						
Merlucciotrema praeclarum (Manter, 1934) Yamaguti, 1971	*Platycephalus indicus*	intestine; stomach	5/23	4.8 (1-18)	n.s.	IEBR
***Stomachicola* Yamaguti, 1934**						
Stomachicola muraenesocis Yamaguti, 1934	*Muraenesox cinereus*	intestine, stomach	9/38	5 (1-26)	n.s.	IEBR
***Tubulovesicula* Yamaguti, 1934**						
Tubulovesicula lindbergi (Layman, 1930) Yamaguti, 1934	*Saurida tumbil*	intestine	1/10	3	n.s.	IEBR
Tubulovesicula trichiuri (Gu & Shen, 1978) Wang, 1989	*Trichiurus lepturus*	intestine	2/20	1.5 (1-2)	n.s.	IEBR
Lecithasteridae Odhner, 1905						
***Aponurus* Looss, 1907**						
Aponurus carangis Yamaguti, 1952	*Selar crumenophthalmus*	intestine	1/5	2	n.s.	IEBR
***Hysterolecithoides* Yamaguti, 1934**						
Hysterolecithoides epinepheli Yamaguti, 1934	*Siganus fuscescens*	intestine	7/64	10 (1-45)	n.s.	IEBR
***Lecithaster* Lühe, 1901**						
Lecithaster confusus Odhner, 1905	*Strongylura strongylura*	intestine	2/8	8.5 (4-13)	MH625968-MH625972; MH625982-MH625986; MH625996-MH626000	FSCEAT; IEBR
Lecithaster mugilis Yamaguti, 1970	*Crenimugil seheli*	intestine	4/41	8.3 (2-20)	LN865007–LN865012; LN865016–LN865021	FSCEAT nos. 60-67-Tr; IEBR
	Ellochelon vaigiensis	intestine	1/3	52	n.s.	IEBR
	Osteomugil engeli	intestine	22/95	15.2 (1-50)		
	Planiliza subviridis	intestine	8/31	11.4 (3-22)		
Lecithaster sayori Yamaguti, 1938	*Hemiramphus marginatus*	intestine	1/15	2	MH625977; MH625991; MH626004	FSCEAT; IEBR
Lecithaster sp.	*Siganus fuscescens*	intestine	1/64	11	n.s.	IEBR

Table 2 (continued)

Parasite species	Fish host	Infection site	No. infected/No. examined	Intensity of infection: mean (range)	GenBank numbers of submitted sequences	Specimen stored
Lepocreadiidae Odhner, 1905						
***Bianium* Stunkard, 1930**						
**Bianium tonkinensis* Nguyen et al., 2014	*Lagocephalus lunaris*	intestine	2/5	30 (10-50)	n.s.	Vietnam National Museum of Nature (VNMN) nos. 2013-2020
***Lepotrema* Ozaki, 1932**						
Lepotrema cylindricum (Wang, 1989) Bray, Cutmore & Cribb, 2018	*Monacanthus chinensis*	intestine	1/4	1	n.s.	IEBR
***Opechona* Looss, 1907**						
Opechona formiae Oshmarin, 1965	*Parastromateus niger*	intestine	3/5	2 (1-3)	n.s.	IEBR
Monorchiidae Odhner, 1911						
***Sinistroporomonorchis* Wee, Cutmore, Pérez-del-Olmo & Cribb, 2020**						
Sinistroporomonorchis lizae (Liu, 2002) Wee, Cutmore, Pérez-del-Olmo & Cribb, 2020	*Liza longimanus*	intestine	2/3	26.5 (3-50)	n.s.	IEBR
Opecoelidae Ozaki, 1925						
***Opecoelus* Ozaki, 1925**						
**Opecoelus haduyngoi* Nguyen, 2012	*Acanthopagrus latus*	intestine	3/3	6 (5-7)	n.s.	IEBR
***Opegaster* Ozaki, 1928**						
Opegaster brevifistula Ozaki, 1928	*Sillago sihama*	intestine	8/14	6.6 (1-15)	n.s.	IEBR
Zoogonidae Odhner, 1902						
***Lecithostaphylus* Odhner, 1911**						
**Lecithostaphylus halongi* Atopkin, Besprozvannykh, Ha, Nguyen & Nguyen, 2022	*Hemiramphus far*	intestine	4/5	2.3 (1-5)	OK636406- OK636407	Scientific Center of the East Asia Terrestrial Biodiversity Far Eastern Branch of Russian Academy of Sciences) No. 194-198-Tr
	Hemiramphus marginatus	intestine	1/15	1	n.s.	IEBR
MONOGENEA						
DACTYLOGYRIDEA BYCHOWSKY, 1937						
Ancyrocephalidae Bychowsky, 1937						
***Hemirhamphiculus* Bychowsky & Nagibina, 1969**						
Hemirhamphiculus armatus Bychowsky & Nagibina, 1969	*Hemiramphus far*	gill	5/5	7 (3-11)	n.s.	IEBR
****Hemirhamphiculus pinguis* (Bychowsky & Nagibina, 1969) Kritsky, 2017	*Hyporhamphus quoyi*	gill	7/28	6.9 (1-23)	n.s.	IEBR
****Hemirhamphiculus similis* Bychowsky & Nagibina, 1969	*Hemiramphus marginatus*	gill	10/15	5.1 (1-12)	n.s.	IEBR

Table 2 (continued)

Parasite species	Fish host	Infection site	No. infected/No. examined	Intensity of infection: mean (range)	GenBank numbers of submitted sequences	Specimen stored
***Ligophorus* Euzet & Suriano, 1977**						
Ligophorus fenestrum Soo & Lim, 2012	*Planiliza melinoptera*	gill	17/83	2.2 (1-5)	n.s.	A.O. Kovalevsky Institute of Marine Biological Research, Russian Academy of Sciences (IMBR); IEBR
	Planiliza subviridis	gill	10/31	6 (1-14)		
Ligophorus hamulosus Pan et Zhang, 1999	*Osteomugil cunnesius*	gill	1/18	50	n.s.	IMBR; IEBR
	Crenimugil seheli	gill	1/41	4		
***Ligophorus leporinus* (Zhang & Ji, 1981) Gussev, 1985	*Crenimugil heterocheilos*	gill	4/157	39.3 (1-80)	n.s.	IMBR; IEBR
	Ellochelon vaigiensis	gill	2/3	19 (15-23)		
	Mugil cephalus	gill	10/35	37 (1-240)		
	Osteomugil engeli	gill	9/95	8.9 (1-27)		
	Planiliza affinis	gill	1/1	1		
	Planiliza planiceps	gill	1/3	1		
***Paradiplectanotrema* Gerasev, Gayevskaya & Kovaleva, 1987**						
Paradiplectanum blairense (Gupta & Khanna, 1974) Domingues & Boeger, 2008	*Sillago sihama*	gill	13/14	31.6 (1-100)	n.s.	IEBR
Paradiplectanotrema trachuri (Kovaljova, 1970) Gerasev, Gayevskaya & Kovaleva, 1987	*Argyrosomus japonicus*	gill	11/12	4.7 (1-14)	n.s.	IEBR
	Johnius carouna	gill	3/5	1.3 (1-2)		
***Tetrancistrum* Goto & Kikuchi, 1917**						
**Tetrancistrum sigani* Goto & Kikuchi, 1917	*Siganus fuscescens*	gill	54/64	9.9 (1-61)	n.s.	IEBR
Dactylogyridae Bychowsky, 1933						
**Dactylogiridae gen. sp.	*Xenentodon cancila*	gill	¼	5	n.s.	IEBR
***Haliotrema* Johnston & Tiegs,1922**						
Haliotrema epinepheli Young, 1968	*Epinephelus sexfasciatus*	gill	5/5	11.8 (3-26)	n.s.	IEBR
Haliotrema holocentri Young, 1968	*Sargocentron rubrum*	gill	13/20	10.2 (2-35)	n.s.	IEBR
Haliotrema ohsntoni Bychowsky & Nagibina, 1970	*Upeneus tragula*	gill	5/10	19 (1-50)	n.s.	IEBR
Haliotrema platycephali Yin & Sproston, 1948	*Platycephalus indicus*	gill	4/23	20.5 (4-36)	n.s.	IEBR
Diplectanidae Monticelli, 1903						
***Calydiscoides* Young, 1969**						
Calydiscoides flexuosus (Yamaguti, 1953) Young, 1969	*Nemipterus japonicus*	gill	9/15	44 (20-60)	n.s.	IEBR
***Murraytrema* Price, 1937**						
Murraytrema pricei Bychowsky & Nagibina, 1977	*Nibea albiflora*	gill	5/8	8.4 (1-17)	n.s.	IEBR

Table 2 (continued)

Parasite species	Fish host	Infection site	No. infected/No. examined	Intensity of infection: mean (range)	GenBank numbers of submitted sequences	Specimen stored
Protogyrodactylidae Johnston & Tiegs, 1922						
***Protogyrodactylus* Johnston & Tiegs, 1922**						
Protogyrodactylus alienus Bychowsky & Nagibina, 1974	*Gerres filamentosus*	gill	2/8	25 (15-35)	n.s.	IEBR
Protogyrodactylus gussevi Bychowsky & Nagibina, 1974	*Terapon jarbua*	gill	1/16	14	n.s.	IEBR
Protogyrodactylus perforatus Bychowsky & Nagibina, 1974	*Terapon jarbua*	gill	1/16	12	n.s.	IEBR
***Protogyrodactylus solidus* Bychowsky & Nagibina, 1974	*Terapon theraps*	gill	½	1	n.s.	IEBR
MAZOCRAEIDEA BYCHOWSKY, 1937						
Allodiscocotylidae Tripathi, 1959						
***Allodiscocotyla* Yamaguti, 1953**						
Allodiscocotyla chorinemi Yamaguti, 1953	*Scomberoides commersonnianus*	gill	4/9	5.8 (1-18)	n.s.	IEBR
***Metacamopia* Lebedev, 1972**						
Metacamopia chorinemi (Yamaguti, 1953) Lebedev, 1984	*Selar crumenophthalmus*	gill	2/5	1	n.s.	IEBR
Axinidae Monticelli, 1903						
***Axine* Abildgaard, 1794**						
Axine hemirhamphae Tripathi, 1959 (syn. *Axine tripathii* Price, 1962)	*Rhynchorhamphus georgii*	gill	11/61	2 (1-3)	n.s.	IEBR
***Neoaxine* Price, 1946**						
**Neoaxine constricta* (Yamaguti, 1938) Price, 1946	*Strongylura leiura*	gill	1/1	2	n.s.	IEBR
	Strongylura strongylura	gill	7/8	9.3 (1-30)	n.s.	IEBR
Diclidophoridae Cerfontaine, 1895						
***Helciferus* Mamaev, 1972**						
Helciferus tenuis Mamaev, 1972	*Coilia rebentischii*	gill	4/10	1.3 (1-2)	n.s.	IEBR
***Heterobothrium* Cerfontaine, 1895**						
***Heterobothrium tonkinense* Bychowsky & Nagibina, 1976	*Lagocephalus lunaris*	gill	1/5	1	n.s.	IEBR
***Papillochoricotyle* Mamaev, 1975**						
***Papillochoricotyle ilishae* Mamaev, 1975	*Ilisha megaloptera*	gill	4/5	10.3 (3-17)	n.s.	IEBR

Table 2 (continued)

Parasite species	Fish host	Infection site	No. infected/No. examined	Intensity of infection: mean (range)	GenBank numbers of submitted sequences	Specimen stored
Gastrocotylidae Price, 1943						
***Pseudaxine* Parona & Perugia, 1890**						
Pseudaxine bychowskyi (Lebedev, 1977) Bouguerche, Tazerouti, Gey & Justine, 2020	*Alepes djedaba*	gill	6/15	11.5 (2-20)	n.s.	IEBR
Pseudaxine trachuri Parona & Perugia, 1889	*Decapterus russelli*	gill	2/10	1	n.s.	IEBR
Gotocotylidae Yamaguti, 1963						
***Cathucotyle* Lebedev, 1968**						
Cathucotyle cathuaui Lebedev, 1968	*Scomberomorus commerson*	gill	5/12	4.2 (3-7)	n.s.	IEBR
Mazocraeidae Price, 1936						
***Mazocraeoides* Price, 1936**						
Mazocraeoides sp.	*Tenualosa thibaudeaui*	gill	3/10	12.7 (1-29)	n.s.	IEBR
***Heteromazocraes* Mamaev, 1981**						
***Heteromazocraes vicinus* (Mamaev, 1975) Mamaev, 1981	*Thryssa dussumieri*	gill	5/17	2.6 (1-5)	n.s.	IEBR
Plectanocotylidae Monticelli, 1903						
***Octoplectanocotyla* Yamaguti, 1937**						
**Octoplectanocotyla* sp.	*Trichiurus lepturus*	gill	8/20	1.4 (1-4)	n.s.	IEBR
Protomicrocotylidae Johnston & Tiegs, 1922						
***Vallisiopsis* Subhapradha, 1951**						
****Vallisiopsis sphyraenae* Yamaguti, 1968	*Sphyraena obtusata*	gill	2/10	1	n.s.	IEBR
***Bilaterocotyloides* Ramalingam, 1961**						
Bilaterocotyloides carangis Ramalingam, 1961	*Megalaspis cordyla*	gill	5/5	13 (6-25)	n.s.	IEBR
Thoracocotylidae Price, 1936						
***Pricea* Chauhan, 1945**						
Pricea multae Chauhan, 1945	*Scomberomorus commerson*	gill	6/12	11.7 (5-23)	n.s.	IEBR
NEMATODA						
RHABDITIDA CHITWOOD, 1933						
Anisakidae Railliet & Henry, 1912						
***Contracaecum* Railliet & Henry, 1912**						
Contracaecum osculatum (Rudolphi, 1802) Baylis, 1920	*Trichiurus lepturus*	intestine	6/20	3.5 (1-10)	n.s.	IEBR
	Scomberoides commersonnianus	intestine	1/9	1		
†*Contracaecum* sp.	*Aurigequula fasciata*	intestine	1/5	1	n.s.	IEBR
Camallanidae Railliet & Henry, 1915						
***Camallanus* Railliet & Henry, 1915**						
†*Camallanus* sp.	*Johnius carouna*	intestine	2/5	1.5 (1-2)	n.s.	IEBR

Table 2 (continued)

Parasite species	Fish host	Infection site	No. infected/No. examined	Intensity of infection: mean (range)	GenBank numbers of submitted sequences	Specimen stored
Cucullanidae Cobbold, 1864						
***Cucullanus* Müller, 1777**						
Cucullanus truttae Fabricius, 1794	*Nibea albiflora*	intestine	1/8	7	n.s.	IEBR
†*Cucullanus* sp.	*Johnius carouna*	intestine	3/5	1.7 (1-2)	n.s.	IEBR
Cystidicolidae Skrjabin, 1946						
***Ascarophis* van Beneden, 1871**						
†*Ascarophis* sp.	*Nibea albiflora*	intestine	1/8	1	n.s.	IEBR
	Platycephalus indicus	intestine	1/23	2		
Physalopteridae Railliet, 1893						
***Heliconema* Travassos, 1919**						
Heliconema longissimum (Ortlepp, 1923)	*Muraenesox cinereus*	intestine	9/38	18.1 (2-54)	n.s.	IEBR
Raphidascarididae Hartwich, 1954						
***Hysterothylacium* Ward & Magath, 1917**						
Hysterothylacium longilabrum Li, Liu & Zhang, 2012	*Siganus fuscescens*	intestine	11/64	5.3 (1-22)	n.s.	IEBR
***Raphidascaris* (*Raphidascaris*) Railliet & Henry, 1915**						
Raphidascaris (*Raphidascaris*) *acus* (Bloch, 1779) Railliet & Henry, 1915	*Ariomma indica*	intestine	1/10	1	n.s.	IEBR
	Argyrosomus japonicus	intestine	4/12	6 (1-20)		
	Nemipterus japonicus	intestine	2/15	2 (2)		
	Sillago sihama	intestine	1/14	1		
†*Raphidascaris* sp.	*Ilisha elongata*	intestine	1/2	1	n.s.	IEBR
	Osteomugil cunnesius	intestine	1/18	1		
	Plotosus lineatus	intestine	1/10	1		
	Selaroides leptolepis	intestine	2/3	3 (3)		
HIRUDINEA						
RHYNCHOBDELLIDA BLANCHARD, 1894						
Piscicolidae Johnston, 1865						
***Oceanobdella* Caballero, 1956**						
***Oceanobdella sexoculata* (Malm, 1863)	*Mugil cephalus*	gill	5/35	2.6 (1-5)	n.s.	IEBR
***Piscicola* Blainville, 1818**						
***Piscicola geometra* (Linnaeus, 1761)	*Planiliza melinoptera*	gill	1/83	2	n.s.	IEBR
COPEPODA						
CYCLOPOIDA BURMEISTER, 1834						
Bomolochidae Claus, 1875						
***Bomolochidae* Claus, 1875**						
Bomolochus sp.	*Decapterus maruadsi*	gill	1/5	1	n.s.	IEBR
***Nothobomolochus* Vervoort, 1962**						
***Nothobomolochus denticulatus* (Bassett-Smith, 1898	*Sphyraena obtusata*		2/10	2.5 (2-3)	n.s.	IEBR
Nothobomolochus sp.	*Mugil cephalus*	gill	7/35	1.4 (1-2)		IEBR

Table 2 (continued)

Parasite species	Fish host	Infection site	No. infected/No. examined	Intensity of infection: mean (range)	GenBank numbers of submitted sequences	Specimen stored
Philichthyidae Vogt, 1877						
***Colobomatus* Hesse, 1873**						
Colobomatus sp.	*Platycephalus indicus*	gill	1/23	4	n.s.	IEBR
ORDER SIPHONOSTOMATOIDA THORELL, 1859						
Caligidae Burmeister, 1835						
***Caligus* Müller, 1785**						
Caligus arii Bassett-Smith, 1898	*Trichiurus lepturus*	gill	2/20	1	n.s.	IEBR
***Caligus eleutheronemi* Shen, 1957	*Leptomelanosoma indicum*	gill	1/2	3	n.s.	IEBR
***Caligus epidemicus* Hewitt, 1971	*Diploprion bifasciatum*	gill	4/12	2 (1-4)	n.s.	IEBR
***Caligus epinepheli* Yamaguti, 1936	*Acanthopagrus latus*	gill	1/3	3	n.s.	IEBR
Caligus lagocephali Pillai, 1961	*Lagocephalus lunaris*	gill	1/5	1	n.s.	IEBR
Caligus laticaudus Shiino, 1960	*Siganus fuscescens*	gill	1/64	1	n.s.	IEBR
Caligus sp.	*Scatophagus argus*	gill	1/7	2	n.s.	IEBR
Hatschekiidae Kabata, 1979						
***Hatschekia* Poche, 1902**						
***Hatschekia* sp.	*Diploprion bifasciatum*	gill	2/12	2 (1-3)	n.s.	IEBR
***Pseudocongericola* Yü, 1933**						
***Pseudocongericola chefoonensis* Yü, 1933	*Muraenesox cinereus*	gill	12/82	6.8 (1-23)	n.s.	IEBR
Lernaeopodidae Milne Edwards, 1840						
***Brachiella* Cuvier, 1830**						
Brachiella trichiuri indica Ho & Do, 1984	*Trichiurus lepturus*	gill	2/20	1	n.s.	IEBR
***Clavellisa* Wilson, 1915**						
***Clavellisa obcordatus* Rangnekar, 1957	*Thryssa dussumieri*	gill	5/17	3 (1-6)	n.s.	IEBR
***Parabrachiella* Wilson, 1915**						
***Parabrachiella brevicapita* (Ho & Do, 1984)	*Nibea albiflora*	gill	1/8	1		IEBR
	Osteomugil cunnesius	gill	1/18	4	n.s.	
	Osteomugil engeli	gill	1/95	1		
Lernanthropidae Kabata, 1979						
***Lernanthropinus* Ho & Do, 1985**						
Lernanthropinus decapteri (Pillai, 1964)	*Decapterus russelli*	gill	1/10	5	n.s.	IEBR
***Lernanthropodes* Bere, 1936**						
Lernanthropodes chorinemi Pillai, 1962	*Scomberoides commersonnianus*	gill	2/9	1	n.s.	IEBR
***Lernanthropus* de Blainville, 1822**						
***Lernanthropus indicus* Pillai, 1967	*Upeneus tragula*	gill	5/10	2.6 (1-4)	n.s.	IEBR

Table 2 (continued)

Parasite species	Fish host	Infection site	No. infected/No. examined	Intensity of infection: mean (range)	GenBank numbers of submitted sequences	Specimen stored
******Lernanthropus otolithi*** Pillai, 1963	*Argyrosomus japonicus*	gill	4/12	3.3 (1-8)	n.s.	IEBR
	Johnius belangerii	gill	4/15	1.3 (1-2)		
	Otolithes ruber	gill	1/5	2		
Lernanthropus polynemi Richiardi, 1881	*Plotosus lineatus*	gill	1/10	2	n.s.	IEBR
Lernanthropus tylosuri Richiardi, in Goggio, 1906	*Strongylura strongylura*	gill	3/8	3 (2-5)	n.s.	IEBR
Lernanthropus villiersi Delamare Deboutteville & Nunes-Ruivo, 1954	*Gerres filamentosus*	gill	1/8	2	n.s.	IEBR
Lernanthropus sp.	*Equulites rivulatus*	gill	1/3	1	n.s.	IEBR
Taeniacanthidae Wilson, 1911						
***Taeniacanthus* Sumpf, 1871**						
******Taeniacanthus lagocephali*** Pearse, 1952	*Monacanthus chinensis*	gill	4/14	3.5 (2-7)	n.s.	IEBR
MALACOSTRACA						
ISOPODA LATREILLE, 1817						
Cymothoidae Leach, 1814						
***Smenispa* Özdikmen, 2009**						
Smenispa irregularis (Bleeker, 1857)	*Terapon jarbua*	gill	1/16	3	n.s.	IEBR
Gnathiidae Leach, 1814						
***Gnathia* Leach, 1814**						
Gnathia sp.	*Cynoglossus bilineatus*	gill	1/9	1	n.s.	IEBR
MYXOZOA						
BIVALVULIDA SHULMAN, 1959						
Ceratomyxidae Doflein, 1899						
***Ceratomyxa* Thélohan, 1892**						
*****Ceratomyxa*** sp.	*Nemipterus japonicus*	gall-bladder	6/15	uncounted	n.s.	IEBR
Coccomyxidae Léger & Hesse, 1907						
***Auerbachia* Meglitsch, 1960**						
*****Auerbachia*** sp.	*Nemipterus japonicus*	gall-bladder	2/15	uncounted	n.s.	IEBR
Myxobolidae Thélohan, 1892						
***Myxobolus* Bütschli, 1882**						
*****Myxobolus*** sp.	*Planiliza subviridis*	muscle	2/31	uncounted	n.s.	IEBR
Myxidiidae Thélohan, 1892						
***Myxidium* Buetschli, 1882**						
*****Myxidium*** sp.1	*Hemiramphus far*	gall-bladder	1/5	uncounted	n.s.	IEBR
***Zschokkella* Auerbach, 1909**						
*****Zschokkella*** sp.	*Nemipterus japonicus*	gall-bladder	1/15	uncounted	n.s.	IEBR
Sphaeromyxidae Lom & Noble, 1984						
***Sphaeromyxa* Thélohan, 1892**						
*****Sphaeromyxa*** sp. 1	*Hemiramphus marginatus*	gall-bladder	3/15	uncounted	n.s.	IEBR

Table 2 (continued)

Parasite species	Fish host	Infection site	No. infected/No. examined	Intensity of infection: mean (range)	GenBank numbers of submitted sequences	Specimen stored
***Sphaeromyxa* sp. 2	*Megalaspis cordyla*	gall-bladder	2/5	uncounted	n.s.	IEBR
Trilosporidae Shulman, 1959						
***Unicapsula* Davis, 1924**						
Unicapsula pyramidata (Naidenova & Zaika, 1970)	*Nemipterus japonicus*	muscle	4/15	uncounted	AB971675-AB971676	IEBR
MULTIVALVULIDA SHULMAN, 1959						
Kudoidae Meglitsch, 1960						
***Kudoa* Meglitsch, 1947**						
***Kudoa monodactyli* Gunter, Cribb, Whipps & Adlard, 2006	*Osteomugil cunnesius*	Muscle	5/95	uncounted	OL339428, OP070006	IEBR
***Kudoa whippsi* Burger & Adlard, 2010	*Osteomugil cunnesius*	Muscle	5/18	uncounted	OL339425, OP070005	IEBR
***Kudoa* sp. 1	*Scomberomorus commerson*	Muscle	4/12	uncounted	n.s.	IEBR
***Kudoa* sp. 2	*Planiliza subviridis*	Muscle	7/31	uncounted	n.s.	IEBR
***Kudoa* sp. 3	*Planiliza subviridis*	Muscle	4/31	uncounted	n.s.	IEBR
***Kudoa* sp. 4	*Osteomugil cunnesius*	Muscle	12/95	uncounted	n.s.	IEBR
***Kudoa* sp. 5	*Osteomugil cunnesius*	Muscle	10/95	uncounted	n.s.	IEBR

Note: *new species described from collected specimens in this survey; **new parasite locality records; ***new host records; †larvae stage; n.s. not sequence

(Valenciennes), were the dominant examined fishes, consistuting 33% of all sampled fishes.

A total of 994 (95.39%) specimens, representing 68 fish species (85%), were infected by one or more parasite taxa (Table 1). On average, each fish species was infected by 3 parasitic groups (range 1-7 groups per host). Trematodes, monogeneans, and crustaceans were the most common parasites, and have been collected from 47, 43, and 29 fish species, respectively. Less than 20 fish species were infected with the other parasite groups, particularly Hirudinea, which was only discovered in 2 fish species. Infection intensity was the highest with monogeneans, with about 11.4 worms per infected fish, followed by trematodes (10.37), and acanthocephalans (10.21). Infection intensity was not measured for myxozoans. The prevalence of infection also did not differ significantly by season (p=0.975), although the prevalence in dry seasons was slightly greater than in rainy seasons (1.01 times).

Diversity of parasites and their classification

Parasites collected from marine fishes in the Cat Ba Archipelago were divided into 8 groups, e.g. acanthocephala, cestode, trematode, monogenea, nematode, hirudinea, crustacean (copepod and isopod), and myxozoa. A total of 162 parasitic species within 107 genera from 60 families, and 15 orders of 9 higher taxa were defined (Table 2). Trematodes were the most diverse group, with 54 identified species, followed by monogeneans (37 species), and copepods (25 species). Hirudinea and isopods only had two species each. Most parasites (138 species) were found in only one fish host, while others were found in 2-6 hosts. The largest host range was found for *Ligophorus leporinus* (monogenean), which was found from 6 fish species, followed by *Paucivitellosus vietnamensis* (trematode), and *Neoechinorhynchus* (*Neoechinorhynchus*) *longinucleatus* (acanthocephalan), which were each found from 5 fish host species. During the survey, twenty new species were described, including 7 acanthocephalans and 13 trematodes; twenty

species were recorded for the first time from the Cat Ba Archipelago, and twenty-two species had new host records reported. Among the 162 parasitic species recorded, 35 were only identified to the genus or higher taxanomic level, including three larval taxa of cestodes, two trematodes, five nematodes, three female crustaceans, two undescribed new species of monogeneans, and 12 unidentified species of myxozoans.

Eighty-one parasite species were found from the intestine and/or stomach, including all species of acanthocephala, cestoda, trematoda, and nematoda. Monogeneans, hirudinea, and crustaceans were collected from the host gills, while myxozoans found in the muscle or gall-bladder.

The prevalence and intensity of each parasite species differed among fish hosts (Table 2). Prevalence ranged from 1.1% to 100%. Parasite abundance, except for myxozoans, ranged from 1 to 69 samples per infected fish.

Discussion

A remarkable 85% of the examined fish species (68 of 80) were infected by 162 distinct parasitic species. Extrapolating from these figures, the projected number of fish parasites among the 361 reported marine fish species in the Cat Ba Archipelago approximates to 730. The number of parasitic species in the current study now accounts for one-third of all parasitic species within and on marine fishes in Vietnam, when compared to the 498 species discovered from 225 fish species by Truong et al. (2022). Additionally, it is worth noting that the mean number of parasitic species per infected fish within the Cat Ba Archipelago surpasses the corresponding figure for Vietnam's entire offshore regions (2.38 versus 2.21), as well as other prominent Pacific Ocean island regions, such as Hawaii (2.2), New Caledonia (1.9), and the Indo West Pacific (1.7) (Rohde, 2005; Justine, 2010; Palm & Bray, 2014).

Despite the diversity of fishes in the Cat Ba Archipelago, only 80 fish species were studied between 2010 and 2023 due to constraints related to procuring fish specimens from the local fishery. Each fisherperson had their distinct familiar fishing grounds which resulted in a relatively stable composition of fish species over the course of the nine sampling periods. Among the 80 species surveyed, the occurrence of individual fish varied significantly. While certain species were encountered only once, represented by a solitary specimen, others exhibited a higher frequency, with counts reaching as high as 95 individuals. For example, the mugilids were the most sampled, with 13 species and 362 examined specimensAlthough only 80 fish species were investigated, 42 species were identified as new hosts of parasites (including 20 new parasitic species and 22 new host records). These findings underscore the endemic nature of the host-parasite interactions observed within the fish population of the Cat Ba Archipelago.

Within the current list of marine fish parasites of Vietnam (Truong et al., 2022), trematodes encompass 214 of the total 498 parasitic species (42.97%). Despite being a major group of parasites in the present study, with 54 species, trematodes only accounted for 33.33% of the total number of parasite species, lower than the average rate throughout coastal Vietnam. Therefore, given the lower identified trematode diversity, and the fact that we described 12 new species and have identified another 4 undescribed new species, it is likely that there is still a significant number of undiscovered trematode taxa.

Truong et al. (2022) documented 117 monogenean species (23.49% of the total) found in Vietnam's marine fishes. However, it's worth noting that the authors didn't incorporate data from various publications by Russian scientists, resulting in the omission of numerous species from their list. This oversight is particularly significant given that Nguyen et al. (2020c) had previously conducted a comprehensive review, listing 220 monogenean species from 152 marine fish species. In the present study, although no new species were described from fish in Cat Ba Archipelago, new species were described from fish in coastal regions nearby. For example, Kritsky et al. (2016) described two new species of *Metahaliotrema* from the spotted scat, *Scatophagus argus,* from off Mong Cai, Quang Ninh province; Nguyen et al. (2016, 2020a) described a new species *Unnithanaxine naresii* from the Pharao flyingfish, *Cypselurus naresii*, and two new species of *Karavolicotyla* from sciaenid fishes from the Gulf of Tonkin; and Nguyen et al. (2020b) described two new species of *Polylabroides*, and one species of *Metacamopia* from the Pacific seabream, *Acanthopagrus pacificus,* from the coast of Mong Cai, off Tien Yen, Quang Ninh

province. Considering the remarkable diversity of fishes and ecosystems within the Cat Ba Archipelago, the exploration of the monogenean fauna, the intricate dynamics of host-parasite relationships, and the evolutionary interactions of hosts and parasites in this region possess immense value for researchers.

According to Truong et al. (2022), there are 17 species of tapeworm reported in marine fishes from Vietnam. Seven cestode species were found in the current study; only three of these seven had been previously found in Veitnam, while the remaining species represent new records for Vietnam. Three species were only identified to a generic level due to the unmatured/larval stage of specimens, including *Bothriocephalus* sp. from the Largehead hairtail, *Trichiurus lepturus*. Yera et al. (2013) found the Asian fish tapeworm *Bothriocephalus acheilognathi* in human stools. Therefore, there is a potential for humans to become infected with *Bothriocephalus* from eating undercooked *T. lepturus*.

A total of 39 acanthocephalan species have been described so far from marine fishes in Vietnam (Nguyen et al., 2021), including 10 species from the Cat Ba Archipelago. Among them, seven species were new, and two species were found from a new host. Only *Neoechinorhynchus* (*Neoechinorhynchus*) *johnii* had been previously reported from the coastal regions of Vietnam (Nguyen et al., 2021). Half of the discovered acanthocephalan species diversity in the Cat Ba Archipelago belongs to the *Neoechinorhynchus*. Although this genus is quite large (~124 described species), only 9 species have been found in Vietnam (Nguyen et al., 2021). According to Nabi et al. (2015) acanthocephalans are a major threat to the health of fishes globally. Nguyen et al. (2021) provided SEM microphotographs showing the serious damage to the intestinal wall caused by the spiny hooks on the proboscis of acanthocephalans, which has a potential to result in host death (Farias et al., 2021).

Marine fish nematodes of the Cat Ba Archipelago are less diverse, with only 10 species detected (6.17%). Five species were identified at the generic level due to them only being found in their larval stage. *Anisakis* nematodes, which can cause human anisakiasis, were not found in the study, although *A. typical* larvae have been reported in South Central and South Coastal Vietnam from various fish species (Hien et al., 2021), which were also examined in the present study. However, we found two other anisakid species (*Contracaecum* spp.), and one raphidascarid species (*Hysterothylacium* sp.); some species within these genera have been reported to infect humans.

In the present study, two species of leech were collected from mugilid fishes, *Oceanobdella sexoculata* and *Piscicola geometra*. Only two other species of leech have been reported in previous studies, *Zeylanicobdella arugamensis* and *Piscicola* sp. from groupers and snappers Truong et al. (2022). Therefore, 4 species of hirudinea in Vietnam marine fishes are known so far.

Crustaceans were the third most diverse group of parasites in this study, comprising 25 copepods and two isopods. Species of two genera, *Caligus* and *Lernanthropus*, were dominant, with seven and six species, respectively. Although there are many reports of anchor worms on the skin of marine fishes, such as *Lepeophtheirus* spp. (Ha et al., 2020), all copepods discovered in the present study were found on the gills of their fish hosts. Truong et al. (2022) provided an inaccurate and underestimated list of crustacean species, with 53 copepod and 5 isopod species, while Ha et al. (2020) provided a more detailed and representative list of 73 species of copepod parasitizing marine fishes.

Chinh et al. (2023) provided an updated list of 51 myxozoa species from fishes in Vietnam, including 38 marine species. Only three of 15 myxozoa species found in the present study were identified to the species-level, the remaining taxa, which may include novel diversity, were only identified to the generic-level. While other genera only have one or two species for the region, *Kudoa* is represented by seven species in the region. Myxozoans are one of the most common and diverse groups of parasites in marine fishes (Mackenzie & Kalavati, 2014), therefore the diversity of myzozoans in the Cat Ba Archipelago may be higher than the current finding and should be a target for further investigation.

Before 2020, there were about 450 fish culture facilities within the inshore water of the Cat Ba Archipelago (Hai Phong Fisheries Sub-Department, 2021). However, due to aquaculture's potential negative environmental and public health impacts (Madsen et al., 2022), the Hai Phong Municipal People's Committee proposed a policy to move the current facilities to areas designated for aquaculture. At present, 95% of aquaculture facilities have been moved to culture designated areas. The

present survey only included wild fish and we did not survey cultured fish. Therefore, future efforts should be made to survey cultured fish, as parasite and pathogen data from cultured fishes could help identify potential risks to food safety and human health. One limitation of our study is that we used visual inspection to detect parasites in the examined fish. Visual inspections, alone, are often insufficients for detecting nematode larvae (Levsen et al., 2005; Llarena-Reino et al., 2012), especially parasites infecting the fish musculature. Therefore, other methods. e.g. artificial digestion, compressor method with illuminated table and UV transillumination, could be applied for future investigations (Celano et al., 2013; Shamsi & Suthar, 2016). Additionally, metacercariae from marine fish were not investigated, and given their potential to harm their fish hosts, should be targets of future studies (Kim et al., 2022).

In conclusion, the present study provides the most current list of parasitic fauna from marine fishes from the Cat Ba Archipelago, a biosphere reserve of the world, in Vietnam. We identified 162 parasitic species from 80 wild marine fish species. The data concerning parasitic fauna presented in this paper enhances our understanding of the broader biodiversity within the Cat Ba Archipelago, which are critical for building baselines for measuring future change.

Author contributions H.H.T.N., H.V.N. and H.M.N: Conceptualization; H.H.T.N., H.V.N., H.V.H., N.N.C., V.T.T.T, V.V.K, T.D.H., P.P.D., S.E.G. and H.M.N: Investigation, Metholodogy, Data curation; H.H.T.N., S.E.G. and H.M.N: Writing - original draft; H.V.N.: Funding acquisition and Project administration; H.V.N. and H.M.N: Supervision; Valdation; All authors: Writing - review & editing.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional, national and international guidelines for the care and use of animals were followed.

References

Allen, G. R. (2009). *Field guide to marine fishes of tropical Australia and South-East Asia*. Western Australian Museum, Perth, Australia.

Amin, O. M., & Ha, V. N. (2011). On four species of echinorhynchid acanthocephalans from marine fish in Halong Bay, Vietnam, including the description of three new species and a key to the species of *Gorgorhynchus*. *Parasitology Research, 109*, 841–847. https://doi.org/10.1007/s00436-011-2310-y

Amin, O. M., Nguyen, V. H., & Ha, D. N. (2011a). First report of *Neoechinorhynchus* (Acanthocephala: Neoechinorhynchidae) from marine fish of the eastern seaboard of Vietnam, with the description of six new species. *Parasite*, *18*, 21–34. https://doi.org/10.1051/parasite/2011181021

Amin, O. M., Heckmann, R., & Ha, N. V. (2011b). Description of two new species of *Rhadinorhynchus* (Acanthocephala, Rhadinorhynchidae) from marine fish in Halong Bay, Vietnam, with a key to species. *Acta Parasitologica*, *56*, 67–77. https://doi.org/10.2478/s11686-011-0004-3

Amin, O. M., Heckmann, R., & Ha, N. V. (2011c). Description of *Heterosentis holospinus* n. sp. (Acanthocephala: Arhythmacanthidae) from the striped eel catfish, *Plotosus lineatus*, in Halong Bay, Vietnam, with a key to species of *Heterosentis* and reconsideration of the subfamilies of Arhythmacanthidae. *Comparative Parasitology*, *78*, 29–38. https://doi.org/10.1051/parasite/2019072

Amin, O. M., Heckmann, R., & Ha, N. V. (2018). Descriptions of *Neorhadinorhynchus nudum* (Cavisomidae) and *Heterosentis paraholospinus* n. sp. (Arhythmacanthidae) (Acanthocephala) from fish along the Pacific coast of Vietnam, with notes on biogeography. *Journal of Parasitology*, *104*, 486–495. https://doi.org/10.1645/17-176

Andres, M. J., Pulis, E. E., Cribb, T. H., & Overstreet, R. M. (2014). Erection of the haploporid genus *Litosaccus* n. g. and its phylogenetic relationship within the Haploporidae Nicoll, 1914. *Systematic Parasitology*, *89*(3), 185–94. https://doi.org/10.1007/s11230-014-9521-4

Atopkin, D. M., Besprozvannykh. V. V., Ngo, H. D., Ha, N. V., Tang, N. V., Ermolenko, A. V., & Beloded, A. Y. (2017a). Morphometric and molecular data of the two digenean species *Lasiotocus lizae* Liu, 2002 (Monorchiidae) and *Paucivitellosus vietnamensis* sp. n. (Bivesiculidae) from mullet fish in Tonkin Bay, Vietnam. *Journal of Helminthology*, *91*, 346–355. https://doi.org/10.1017/S0022149X16000389

Atopkin, D. M., Besprozvannykh. V. V., Beloded A. Yu., Ngo, H. D., Ha, N. V., & Tang, N. V. (2017b). Phylogenetic relationships of Hemiuridae (Digenea: Hemiuroidea) with new morphometric and molecular data of *Aphanurus mugilis* Tang, 1981 (Aphanurinae) from mullet fish of Vietnam. *Parasitology International*, *66*, 824–830. https://doi.org/10.1016/j.parint.2017.09.009

Besprozvannykh, V. V, Atopkin, D. M., Ngo, H. D., Ermolenko, A. V., Ha, N. V., Tang, N. V., & Beloded, A. Yu. (2016). Morphometric and molecular analyses of two digenean species from the mullet: *Haplosplanchnus pachysomus* (Eysenhardt, 1892) from Vietnam and *Provitellotrema crenimugilis* Pan, 1984 from the Russian southern Far East. *Journal of Helminthology*, *90*, 238–244. https://doi.org/10.1017/S0022149X15000280

Besprozvannykh, V. V., Atopkin, D. M., Ngo, H. D., Ermolenko, A. V., Ha, N. V., Tang, N. V., & Beloded, A. Y. (2017). Morphometric and molecular analyses of two

digenean species in mugilid fish: *Lecithaster mugilis* Yamaguti, 1970 from Vietnam and *L. sudzuhensis* n. sp. from southern Russian Far East. *Journal of Helminthology*, *91*(3), 326–331. https://doi.org/10.1017/S0022149X16000201

Besprozvannykh, V. V., Atopkin, D. M., Ngo, H. D., Ha, N. V., Tang, N. V., & Beloded, A. Yu. (2018). Morphometric and molecular analyses of two digenean species from the mullet: *Skrjabinolecithum spinosum* n. sp. from the Russian southern Far East and *Unisaccus tonkini* n. sp. from Vietnam. *Journal of Helminthology*, *92*(6), 713–724. https://doi.org/10.1017/S0022149X17000943

Besprozvannykh, V. V., Tatonova, Yu. V., & Shumenko, P. G. (2019). Life cycle, morphology of developmental stages of *Metorchis ussuriensis* sp. nov. (Trematoda: Opisthorchiidae), and phylogenetic relationships of other opisthorchiids. *Journal of Zoological Systematics and Evolutionary Research*, *57*, 24–40. https://doi.org/10.1111/jzs.12230

Besprozvannykh. V. V., Atopkin, D. M., Ngo, H. D., Beloded, A. Yu., Ermolenko, A. V., Ha, N. V., & Tang, N. V. (2015). The Trematode *Skrjabinolecithum spasskii* Belous, 1954 (Digenea: Haploporidae), a mullet parasite (Mugilidae) from Peter the Great Bay of the Sea of Japan and from Vietnamese waters of the Gulf of Tonkin: Morphology and molecular data. *Russian Journal of Marine Biology*, *41*, 267–275. https://doi.org/10.1134/S1063074015040021

Buchmann, K. (2007). *An introduction to fish parasitological methods*. Biofolia, Denmak.

Celano, G. V., Paparella, A., Fransvea, A., Balzaretti, C., & Celano, G. (2013). Rapid mehod for detection of Anisakidae larva in marine fishes, based on UV transillumination. *International Journal of Bioscience, Biochemistry and Bioinformatics*, *3*(4), 392–394.

Chinh, N. N., Ha, N. T. H., Doanh, P. N., Eiras, J. C., Whipps, C. M., & Shirakashi, S. (2023). Synopsis of myxosporean species (Cnidaria: Myxozoa) parasitizing fishes from Vietnam. *Systematic Parasitology*, *100*(4), 325–344. https://doi.org/10.1007/s11230-023-10090-8

Dmitrieva, E. V., Garasev, P. I., Kolpakov, N. V., Nguyen, V. H., & Ha, D. N. (2013). On monogeneans (Plathelminthes, Monogenea) fauna of marine fishes in Vietnam. III. *Ligophorus* spp. from species of mullets (Pisces, Mugilidae). *Bulletin of the Pacific Ocean Fisheries Scientific Research Center*, *172*, 224–236. [in Russian].

Dmitrieva, E. V., Vodiasova, E., Ermolenko, A., Nguyen, V. H., Ha, D. N., & Nguyen, M. H. (2018). Morphological and molecular characteristic of *Ligophorus fenestrum* (Platyhelminthes: Monogenea) from new host-*Planiliza melinopterus* (Actinopterygii: Mugilidae) in the Gulf of Tonkin off Vietnam. Contemporary Parasitology-Major Trends and Challenges. Proceedings of the VI Congress of the Society of Parasitologists, Russia: International Conference, October 15–19, Saint Petersburg, Russia.

Farias, C. F. S., Brandão, F. R., de Alexandre Sebastião, F., de Melo Souza, D. C., Monteiro, P. C., Majolo, C., & Chagas, E. C. (2021). Albendazole and praziquantel for the control of *Neoechinorhynchus buttnerae* in tambaqui (*Colossoma macropomum*). *Aquaculture International*, *29*(4), 1495–1505. https://doi.org/10.1007/s10499-021-00687-5

Folmer, O., Black, M., Hoeh, W., Lutz, R., & Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, *3*(5), 294–299.

Galazzo, D.E., Dayanandan, S., Marcogliese, D.J., McLaughlin, J.D. (2002). Molecular systematics of some North American species of *Diplostomum* (Digenea) based on rDNA-sequence data and comparisons with European congeners. *Canadian Journal of Zoology*, *80*, 2207–2217. https://doi.org/10.1139/Z02-198

Garasev, P. I., Dmitrieva, E. V., Ha, D. N., Kolpakov, N. V., & Nguyen, V. H. (2011a). On monogeneans (Plathelminthes, Monogenea) fauna of marine fishes in Vietnam. I. *Ligophorus* spp. from *Valimugil engeli* Bleeker (Pisces, Mugilidae). *Bulletin of the Pacific Ocean Fisheries Scientific Research Center*, *165*, 196–208. [in Russian].

Garasev, P. I., Dmitrieva, E. V., Ha, D. N., Kolpakov, N. V., & Nguyen, V. H. (2011b). On monogeneans (Plathelminthes, Monogenea) fauna of marine fishes in Vietnam. II. *Ligophorus* spp. from *Valimugil seheli* (Forsskål) (Pisces, Mugilidae). *Bulletin of the Pacific Ocean Fisheries Scientific Research Center*, *165*, 209–215. [in Russian].

Ha, D. N., Nikitich, K. V., Kovaleva, N. N., Nguyen, V. H., & Nguyen, V. T. (2020). *Copepods on marine fish in Vietnam*. Science and Technology Publishing House, Hanoi, Vietnam. [in Vietnamese].

Hai Phong Fisheries Sub Department (2021). Aquaculture in Cat Ba in line with the sustainable and environmentally friendly direction. https://vietnamagriculture.nongnghiep.vn/aquaculture-in-cat-ba-in-line-with-the-sustainable-and-environmentally-friendly-direction-d310889.html. Access on 29 July 2023.

Hien, H. V., Dung, B. T., Ngo, H. D., & Doanh, P. N. (2021). First morphological and molecular identification of third-stage larvae of *Anisakis typica* (Nematoda: Anisakidae) from marine fishes in Vietnamese water. *Journal of Nematology*, *53*, e2021–10. https://doi.org/10.21307/jofnem-2021-010

Hoffman, G. L. (1999). *Parasites of North American Freshwater Fishes*. Cornell University Press, Ithaca.

Huong, N. K. (2001). Marine fishes: Amphioxi, Chondrichthyes, Chondrostei. In: Thanh, D. N., Huynh, D. H., Cao, V. S., Nguyen, T. L., Le, X. H., Thai, T. B., Nguyen, V. S., Ta, H. T. (eds.) *Fauna of Vietnam*, vol. 12. The Science and Technique Publishing House, Hanoi, Vietnam. [in Vietnamese].

Justine, J. L. (2010). Parasites of coral reef fish: how much do we know? With a bibliography of fish parasites in New Caledonia. *Belgian Journal of Zoology*, *140*, 155–190.

Kabata, Z. (1979). *Parasitic Copepoda of British fishes*. The Ray Society, London.

Kazachenko, V. N., Kovaleva, N. N., Ngo, H. D., Ha, N. V., & Thanh, N. V. (2014a). Redescription of three caligid species of the genus *Caligus* Müller, 1785 (Copepoda: Caligidae), parasites of marine fish *Decapterus* sp. (Perciformes: Carangidae) from Tonkin Gulf, Vietnam. *Academia Journal of Biology*, *36*, 1–11. https://doi.org/10.15625/0866-7160/v36n1.4513

Kazachenko, V. N., Kovaleva, N. N., Nguyen, V. T., & Ngo, H. D. (2014b). Taxonomic review of the parasitic copepod

(Crustacea: Copepoda) fish in Vietnam. *Scientific Journal of Dalrybvtuz*, *31*, 20–30.

Kazachenko, V. N., Kovaleva, N. N., Nguyen, V. T., & Ngo, H. D. (2017). Three new species and one new genus of parasitic copepods (Crustacea: Copepoda) from fishes of the South China Sea. *Russian Journal of Marine Biology*, *43*, 264–269. https://doi.org/10.1134/S1063074017040058

Kim, V. V., Nguyen, H. M., Greiman, S. E., Nguyen, H. V., Nguyen, C. N., Vu, M. D., Hoai, T. D., & Madsen, H. (2022). Molecular and morphological characterization of *Dollfustrema bagarii* (Digenea: Bucephalidae) metacercariae from aquaculture channel catfish (*Ictalurus punctatus*) in northern Vietnam. *Journal of Fish Diseases*, *45*(8), 1165–1171. https://doi.org/10.1111/jfd.13651

Kritsky, D. C., Leiby, P. D., & Kayton, R. J. (1978). A rapid stain technique for the haptoral bars of *Gyrodactylus* species (Monogenea). *Journal of Parasitology*, *64*, 172–174. https://doi.org/10.2307/3279642

Kritsky, D. C., Nguyen, H. V., Ha, N. D., & Heckmann, R. A. (2016). Revision of *Metahaliotrema* Yamaguti, 1953 (Monogenoidea: Dactylogyridae), with new and previously described species from the spotted scat *Scatophagus argus* (Linnaeus) (Perciformes: Scatophagidae) in Vietnam. *Systematic Parasitology*, *93*, 321–335. https://doi.org/10.1007/s11230-015-9621-9

Levsen, A., Lunestad, B. T., & Berland, B. (2005). Low detection efficiency of candling as a commonly recommende inspection method for nematode larvae in the flesh of Pelagic fish. *Journal of Food Protection*, *68*(4), 828–832.

Littlewood, D. T. J., & Olson, P. D. (2001). Small subunit rDNA and the Platyhelminthes: signal, noise, conflict and compromise. In Littlewood, D. T. J., & Bray, R. A. (eds) *Interrelationships of Platyhelminthes* (pp. 262–278). Taylor & Francis, London.

Littlewood, D. T. J., Curini-Galletti, M., & Herniou, E.A. (2000). The interrelationships of Proseriata (Platyhelminthes: seriata) flatworms tested with molecules and morphology. *Molecular Phylogenetics and Evolution*, *16*, 449–466. https://doi.org/10.1006/mpev.2000.0802

Llarena-Reino, M., Gonzáles, A. F., Vello, C., Outeiriño, L., & Pascual, S. (2012). The accurary of visual inspection for preventing risk of *Anisakis* spp. infection in unprocess fish. *Food Control*, *23*, 54–58. https://doi.org/10.1016/j.foodcont.2011.06.010

Lom, J., & Arthur, J. R. (1989). A guideline for preparation of species descriptions in Myxosporea. *Journal of Fish Diseases*, 12, 151–156. https://doi.org/10.1111/j.1365-2761.1989.tb00287.x

Mackenzie, K., & Kalavati, C. (2014). Myxosporean parasites of marine fishes: their distribution in the world's oceans. *Parasitology*, *141*, 1709–1717. https://doi.org/10.1017/S0031182014001425

Madsen, H., Nguyen, M. H., Lanza, G. R., & Stauffer, J. R. (2022). A One Health approach relative to trematode-caused diseases of people and animals associated with aquaculture. *Reviews in Fisheries Science and Aquaculture*, *30*(4), 542–566. https://doi.org/10.1080/23308249.2022.2090830

Nabi, S., Tanveer, S., Ganaie, S. A., Ahad, S., Niyaz, U., & Abdullah, I. (2015). Acanthocephalan infestation in fishes-A review. *Journal of Zoology Studies*, *2*(6), 33–38.

Nguyen, H. M., Nguyen, H. V., & Tatonova, Y. V. (2020a). Two new species of *Karavolicotyla* (Unnithan, 1957) (Monogenea: Heteraxinidae): parasites of two sciaenid fishes (Perciformes) from Vietnam. *Raffles Bulletin of Zoology*, *68*, 434–440. https://doi.org/10.26107/RBZ-2020-0059

Nguyen, H. V., Nguyen, H. M., Ha, N. D., Chinh, N. N., Thanh, B. N., Sinh, X. L., Tatonova, Y., & Greiman, S. E. (2020b). Five monogenean species (Allodiscocotylidae, Heteromicrocotylidae, Microcotylidae) from the Pacific seabream *Acanthopagrus pacificus* (Perciformes: Sparidae) in the Gulf of Tonkin off Vietnam, with descriptions of three new species. *Folia Parasitologica*, *67*, 028. https://doi.org/10.14411/fp.2020.028

Nguyen, H. M., Nguyen, H. V., & Ha, N. D. (2020c). An updated list of monogenoidea from marine fishes of Vietnam. *Academia Journal of Biology*, *42*(2), 1–27. https://doi.org/10.15625/2615-9023/v42n2.14819

Nguyen, H. M., Nguyen, H. V., Bui, T. N., & Ha, N. D. (2016). Two new axinid species (Monogenea: Axinidae) from the Pharao flyingfish *Cypselurus naresii* (Günther) (Beloniformes: Exocoetidae) in the Gulf of Tonkin off Vietnam. *Systematic Parasitology*, *93*, 387−394. https://doi.org/10.1007/s11230-016-9635-y

Nguyen, H. V., Ha, D. N., Tran, T. B., & Nguyen, H. M. (2021). *Acanthocephalans from marine fish in Vietnam*. The Science and Technology Publishing House, Hanoi. Vietnam. [in Vietnamese].

Palm, H. W., & Bray, R. A. (2014). *Marine fish parasitology in Hawaii*. Westarp & Partner Digitaldruk, Hohenwarsleben, Germany.

Phung, N. H. (2001). Marine fishes: Elopiformes, Anguilliformes, Clupeiformes, and Gonorynchiformes. In: Thanh, D. N., Huynh, D. H., Cao, V. S., Nguyen, T. L., Le, X. H., Thai, T. B., Nguyen, V. S., & Ta, H. T. (eds.) *Fauna of Vietnam,* vol 10. The Science and Technique Publishing House, Hanoi, Vietnam. [in Vietnamese].

Rohde, K. (2005). *Marine parasitology*. CSIRO Publishing, Victoria, Australia

Sawyer, R. T., Lawler, A. R., & Overstreet, R. M. (1975). Marine leeches of the eastern United States and the Gulf of Mexico with a key to the species. *Journal of Natural History*, *9,* 633–667. https://doi.org/10.1080/00222937500770531

Shamsi, S., & Suthar, J. (2016). A revised method of examining fish for infection with zoonotic nematode larvae. *International Journal of Food Microbiology*, *227*, 13–16. https://doi.org/10.1016/j.ijfoodmicro.2016.03.023

Thanh, T. D., San, B. Q., Can, N. V., Lan, T. D., Quan, N. V., Dieu, L. V., Thu, N. T., Tu, T. A., & Anh, N. T. K. (2015). *Nature and environment in Haiphong coastal zone*. The Publishing House of Nature Science and Technology, Hanoi, Vietnam. [in Vietnamese].

Thi, N. N. (2008). *The marine fishes of Vietnam: Perciformes*. Science and Technique Publishing House, Hanoi, Vietnam. [in Vietnamese].

Thung, D. C., Ngai, N. D., Thao, D. V., Sinh, N. V., & Dong, D. M. (2019). Marine biodiversity in Ha Long bay and Cat Ba Archipelago. *Vietnam Journal of Marine Science and Technology*, *19*(3), 363–369. https://doi.org/10.15625/1859-3097/19/3/13174

Tkach, V. V., Littlewood, D. T. J., Olson, P. D., Kinsella, J. M., & Swiderski, Z. (2003). Molecular phylogenetic analysis of the Microphalloidea Ward, 1901 (Trematoda: Digenea). *Systematic Parasitology*, *56*, 1–15. https://doi.org/10.1017/S0022149X16000201

Truett, G. E., Heeger, P., Mynatt, A. A., Walker, J. A., & Warman, M. L. (2000). Preparation of PCR-quality mouse genomic DNA with hot sodium hydroxide and tris (HotSHOT). *BioTechniques*, *29*, 52–54. https://doi.org/10.2144/00291bm09

Truong, V. T., Ngo, H. T. T., Bui, T. Q., Palm, H. W., & Bray, R. A. (2022). Marine fish parasites of Vietnam: a comprehensive review and updated list of species, hosts, and zoogeographical distribution. *Parasite*, *29*, 36. https://doi.org/10.1051/parasite/2022033

Yera, H., Kuchta, R., Brabec, J., Peyron, F., & Dupouy-Camet, J. (2013). First identification of eggs of the Asian fish tapeworm *Bothriocephalus acheilognathi* (Cestoda: Bothriocephalidea) in human stool. *Parasitology International*, *62*(3), 268–271. https://doi.org/10.1016/j.parint.2013.02.001