Reproductive strategies of parasitic flatworms (Platyhelminthes, Monogenea): the impact on parasite management in aquaculture

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Abstract

Disease management is crucial for the global growth of aquaculture. Parasitic monogeneans present a high risk for finfish aquaculture industries and have been associated with reduced growth, morbidity and mortality. Monogeneans are extremely fecund and exhibit short generation times which can result in exponential population growth. Information on the reproductive biology of specific monogenean species can enable strategically timed treatments to break parasite life cycles. However, the diversity of reproductive strategies (oviparity, viviparity and self-fertilisation) presents considerable barriers in disease management. In addition, environmental conditions such as seasons, water temperature and salinity also influence parasite life cycles, including generation time, fecundity, egg embryonated period and age at sexual maturity. This review examines the diversity of reproductive strategies exhibited by monogenean parasites and the influence of environmental parameters on parasite life cycles. Various parasite management strategies including mechanical, biological and chemical treatments are evaluated.

Keywords Reproduction · Monogenea · Parasites · Aquaculture · Management

Introduction

Global aquaculture production has grown tremendously over the six decades, from a production of less than one million tonnes in 1950s to 32.4 million tonnes in 2000 and 73.8 million

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tonnes in 2014 (FAO 2011, 2016; Subasinghe et al. 2009). Aquaculture is the fastest-growing food producing sector and must meet a growing demand for high-quality sea food. Seafood production for fisheries is at or near its peak (Lucas and Southgate 2012). World aquaculture production of fish accounted for 44.1% of total production from capture fisheries and aquaculture in 2014 (FAO 2016).

Confining organisms in aquaculture systems (e.g. ponds, sea cages and tanks) can create several stressors including overcrowding, oxygen deficiency, aggression and nutritional deficiency. Moreover, handling, waste products, unfavorable lighting, salinity and temperature may lead to immune compromise and increase susceptibility to diseases (Bauer et al. 1973; Lucas and Southgate 2012; Thoney and Hargis 1991). Many disease problems occur in aquaculture and the aquarium industry including viral, bacterial, fungal and parasitic diseases (Whittington and Chisholm 2008; Woo and Gregory 2014; Woo 2006). However, metazoan ectoparasites, especially monogeneans, often cause considerably more significant losses in finfish aquaculture (Ernst et al. 2002; Shinn et al. 2015). In Australia, *Neobenedenia* sp. caused outbreak in the Hinchinbrook Channel in 2000 resulting in mass mortality (fifty tonnes) of Barramundi, *Lates calcarifer*, worth AU $500,000 (Deveney et al. 2001). In 2011, *Neobenedenia* sp. was associated with a disease outbreak of wild Barramundi in Gladstone, Horbour, causing the red and cloudy eyes, skin discolouration, loss of scales, skin damage and lesions (Poiner et al. 2012). The data on economic impacts of aquatic parasites on global finfish production conducted by Shinn et al. (2015) revealed that monogenean parasites contributed significantly for production loss and the economic loss for aquaculture sector in many countries. For example, *N. melleni* was reported to cause 40% mortality for Cobia (*Rachycentron canadum*) cultured in Taiwan in 2001 and the equivalent production loss was estimated 284 million tons. In 2003, two ectoparasites *Benedenia seriolae* and *Zeuxapta seriolae* caused massive mortalities (39 million tons) for Greater amberjack (*Seriola dumerili*). In Japan, the funding for controlling *Benedenia seriolae* infecting the yellowtail (*Seriola quinqueradiata*) in 2001 accounted for more than 20% value of total fish production (33,637 million tons or $214 million). Currently, *Neobenedenia melleni* caused high mortality for this fish and this country has spent over $200 million for control and management this disease (Shinn et al. 2015).

Monogeneans are common ectoparasitic flatworms of marine, brackish and freshwater fishes and are the most diverse ectoparasites of fishes (Buchmann and Bresciani 2006; Whittington and Chisholm 2008). Monogeneans generally live on the external surfaces or body surfaces such as the skin, fins, head, gills and eyes as well as oral and branchial cavities (Whittington and Chisholm 2008; Figs. 1 and 2).

Although some monogenean species live in internal sites with openings to the exterior (urogenital system), very few species infect the digestive tract, heart, kidneys or blood vessels. The haptor is the main organ that monogeneans use to attach to the fish and is the main morphological feature of monogeneans to distinguish this class from their wholly parasitic flatworm relatives, the cestodes and digeneans. Monogeneans are classified into two subclasses: Monopisthocotylea and Polyopisthocotylea (Fig. 3; Whittington and Chisholm 2008).

The division into two subclasses is primarily based on microhabitat, diet, parasite mobility and haptor morphology. Monopisthocotyleans are highly mobile and readily move across epithelial surfaces, feeding on epithelial cells and mucus (Whittington 2005), while polyopisthocotyleans tend to infect fish gills, consume a diet of blood and generally do not
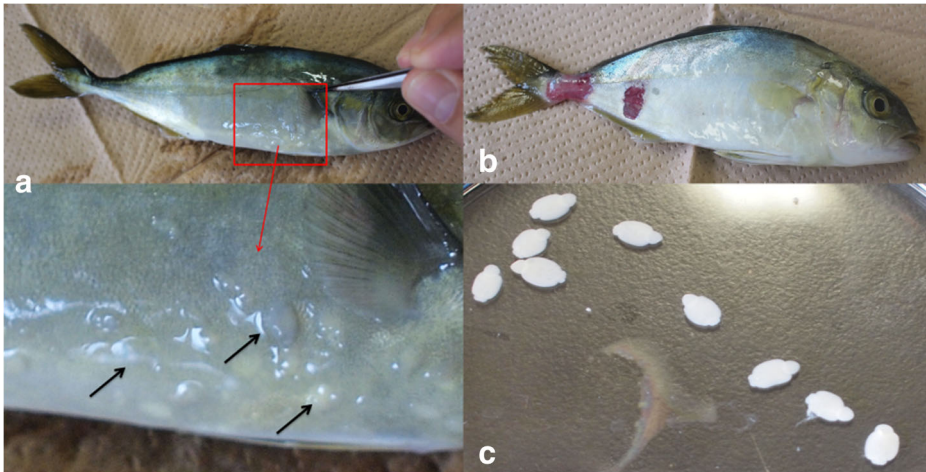
Fig. 1 Monogenean *Benedenia seriolae* (Capsalidae) infecting on skin of yellowtail (*Seriola quinqueradiata*). **a** High density of *B. seriolae* infecting fish. **b** Affected fish with erosion and haemorrhage on skin. **c** Adult *B. seriolae* separated from affected fish and immersed in freshwater

move across large distances, especially in the adult phase (Hayward 2005). There are more than 3500 monogenean species currently described including approximately 1000 marine polyopisthocotylean species (Hayward 2005) and 2500 monopisthocotylean species (Whittington 2005). Monogeneans exhibit a direct life cycle, meaning that only a single host species is required to complete the life cycle. Consequently, monogeneans are widespread in aquaculture, including closed, semi-closed and open systems. However, the potential for
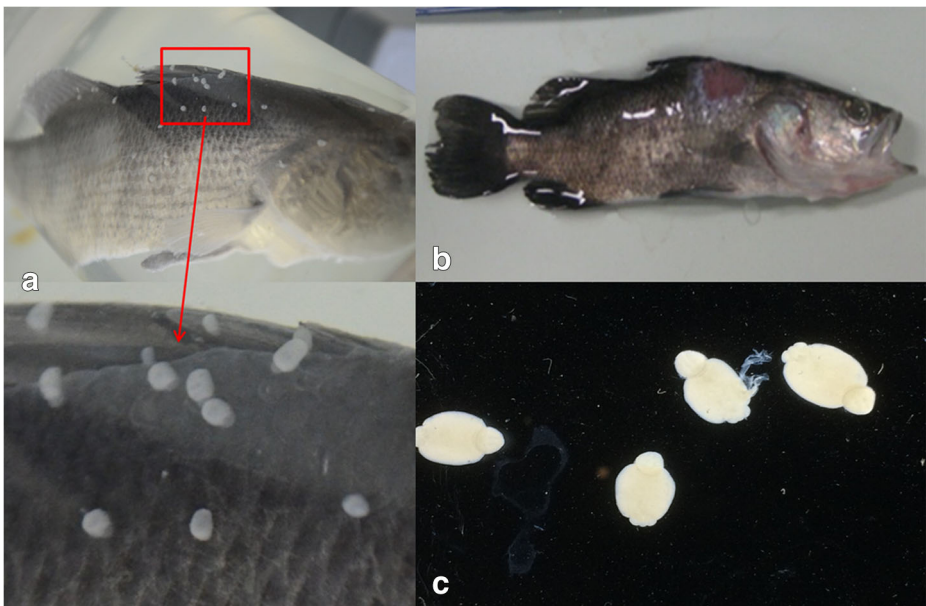

Fig. 2 Monogenean *Neobenedenia* sp. (Capsalidae) infecting on skin and eyes of Barramundi (*Lates calcarifer*). **a** High density of *Neobenedenia* sp. infecting fish. **b** Affected fish with erosion and haemorrhage on skin and broken in the eyes. **c** Adult *Neobenedenia* sp. separated from affected fish and immersed in freshwater
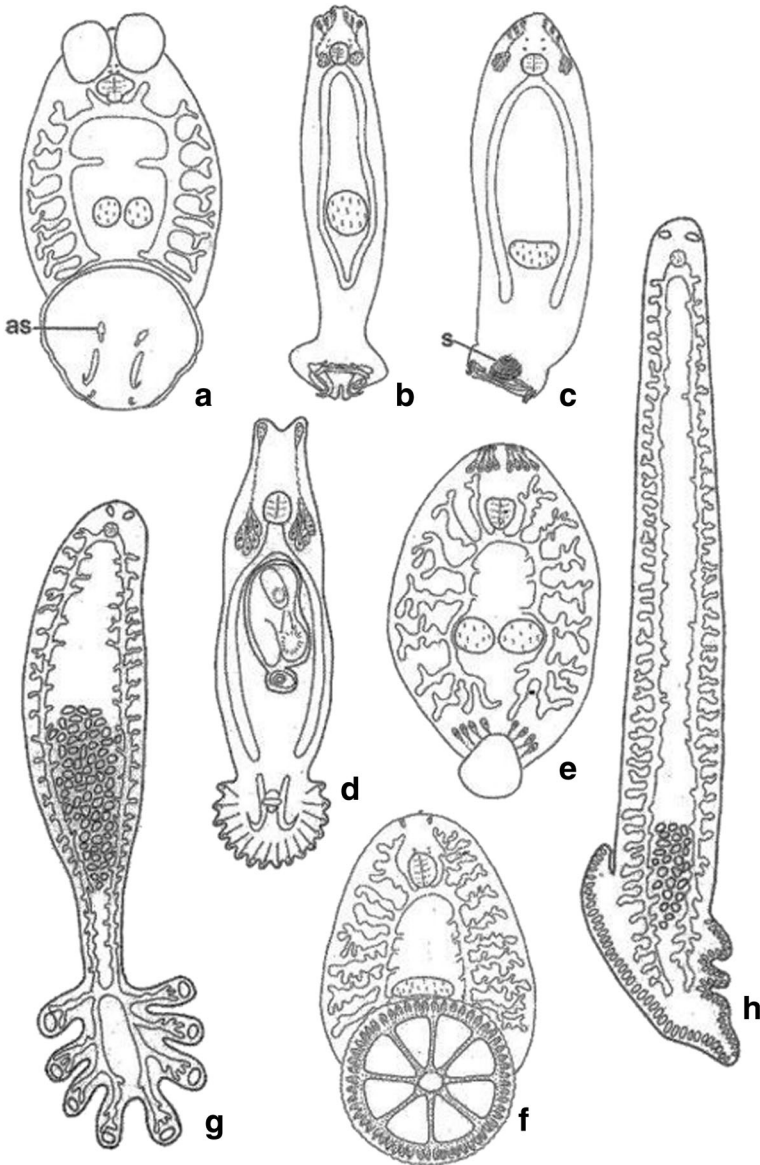
Fig. 3 Morphology of some monogeneans adapted from Whittington and Chisholm 2008; Monopisthocotylea (**a**–**f**): **a** *Benedenia seriolae* (Capsalidae), **b** *Haliotrema abaddon* (dactylogyridae), **c** *Diplectanum aequans* (Diplectanidae), **d** *Gyrodactylus salaris* (Gyrodactylidae), **e** *Dermophthirius* sp. (Microbothriidae), **f** *Dendromonocotyle* sp. (Monocotylidae); Polyopisthocotylea (**g**, **h**): **g** *Neoheterobothrium hirame* and **h** *Zeuxapta seriolae* (Heterraxinidae)

expansion of our knowledge about monogeneans is truly in the future because almost monogeneans investigated up to morphology levels and many others still be lack of reproductive characteristics. Moreover, only small percentage of monogeneans had been investigated, for example, only in the Southeast Asian, 8% of monogenean species are known (Lim 1998). Consequently, many new species await discovery and description.

This review will examine mechanisms of reproduction of monogeneans infecting fish, factors effects to reproduction and current methods used to manage epizootics to facilitate effective management for aquaculture in the future.

Reproduction strategies

Monogeneans are hermaphroditic, with individual worms possessing both male and female compulatory organs (Whittington and Chisholm 2008). The direct life cycle of monogeneans is the most important characteristic for the fast development of outbreaks in aquaculture. Various reproductive strategies have been observed in monogeneans including oviparity, viviparity and self-fertilisation (Buchmann and Bresciani 2006; Buchmann and Uldal 1997; Hoai and Hutson 2014; Ogawa 2002; Whittington and Chisholm 2008). Most monogeneans are oviparous, releasing a large number of eggs into aquatic environment (Fig. 4; Table 1) while a few species are viviparous (Fig. 5; Table 1), in which adults can give birth to live young and several generations can occur within an individual parasite (Whittington and Chisholm 2008). Self-fertilisation is a strategy commonly seen in parasitic platyhelminths where low parasite burdens occur in host populations or where there may be a high frequency of single parasite infection (Haag et al. 1999; Jackson and Tinsley 1988; Stunkard 1957). At least four species of monogeneans in the bladders of amphibians and one infecting fish are capable of producing viable eggs in isolation (Combes 1972; Hoai and Hutson 2014; Jackson and Tinsley 1988; Tinsley and Owen 1975). Whittington and Horton (1996) observed the penis of one *N. melleni* lodged in its own uterus. Self-insemination has been observed in live specimens of *Neobenedenia girellae* (Ogawa et al. 2014) and *Heterobothrium okamotoi*
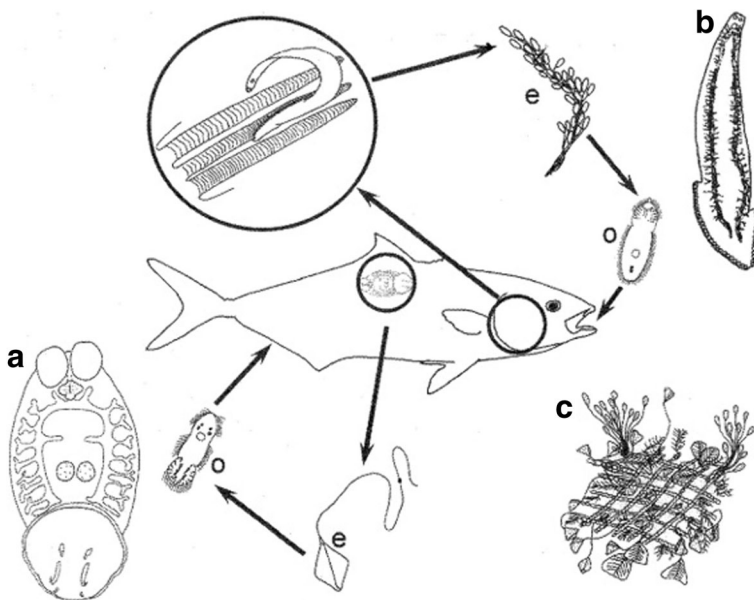

Fig. 4 Oviparity. Life cycle of *Benedenia seriolae* (Monopisthocotylea) (A) and *Zeuxapta seriolae* (Polyopisthocotylea) (B). Eggs (e) hatch to release oncomiracidium (o). Eggs may tangle on filamentous or leafy algae (C). Adapted from Whittington and Chisholm (2008)

Table 1 Monogeneans causing diseases in aquaculture and their reproductive strategies

Subclasses/family	Host	Macro habitat	Micro habitat	Strategy	Reproductive characteristics and life cycle	Reference
Monopisthocotyleans Family Dactylogyridae						
Dactylogyrus vastator	Common carp Goldfish	Freshwater	Gills	Oviparous	Eggs embryonate and hatch within 2–3 days; Oncomiracidia phase is shorter than 24 h, total post-larval development and the adult worm was 10 days at 24–28 °C.	(Bauer et al. 1973)
Dactylogyrus extensus	Common carp goldfish	Freshwater	Gills	Oviparous	Eggs embryonate and hatch within 3 days (22–25, 8–9 days at 16–17. Reach sexual maturity and laid eggs at 6–7 days at 24–25 °C after oncomiracida infection.	(Prost 1963)
Dactylogyrus minutus	Common carp	Freshwater	Gills	Oviparous	-	(Buchmann and Bresciani 2006)
Dactylogyrus lamellatus	Grass carp	Freshwater	Gill filaments	Oviparous	Each adult worm can produce 2–4 eggs/h. Eggs hatch at 5–7 days at 15 °C, 1–1.5 days at 28.5–29.5 °C. Oncomiracidia swimming freely 2–3 h, sexual maturity 5–8 days after. Eggs could withstand low temperatures and hibernate at the bottom of dried ponds during the winter.	(Buchmann and Bresciani 2006; Molnar 1971; Musselius and Ptashuk 1970)
Dactylogyrus ctenopharyng-odonis	Grass carp	Freshwater	Gill filaments and lamellae	Oviparous	Temperature dependent, occurs in warm seasons.	(Bauer et al. 1973)
Dactylogyrus hypophthalmi-chthys	Silver carp	Freshwater	Gill filaments	Oviparous	Similar to other dactylogyrids, temperature dependent.	(Buchmann and Bresciani 2006)
Dactylogyrus aristichthys	Bighead carp	Freshwater	Gill filaments	Oviparous	Fast egg hatching: 2 days at 30 °C, 15–16 days at 5–8 °C, 10 days at 12 °C. Larvae swimming freely 2–11 h in water and full development took 11–13 days at 17–23 °C.	(Musselius 1968)
Acolpeteron ureteroecetes	Largemouth bass	Freshwater	Urinary, urinary bladder systems, ureters of teleosts	Oviparous	Eggs hatched after 26 h	(Reimschuessel et al. 2011)

Table 1 (continued)

Subclasses/family	Host	Macro habitat	Micro habitat	Strategy	Reproductive characteristics and life cycle	Reference
Family Pseudodactylogyridae						
P. anguillae P. bini	Anguillid eel, Japanese eel	Fresh and Brack-ish water	Different microhabitat in the gill apparatus and posterior kidneys	Oviparous	Each worm produces up < 24 egg/day, hatch within 1–2 days and reach sexual maturity after 1 week at 25 °C. Worm may survive more than 60 days	(Buchman 1997)
Family Ancyrocephalidae						
A. vistulensis	European catfish (Silurus glanis)	Freshwater	Gills	-	-	(Székely and Molnár 1990)
Dawestrema cycloancistri-um	Pirarucu (Arapaima gigas)	Freshwater	Gills	Oviparous	-	(Buchmann et al. 1994)
Family Tetraonchidae						
Tetraonchus awakurai	Masou salmon	Freshwater	The lower and middle part of gill filament	Oviparous	Egg hatched to oncomiracidia and transmission occurred as temperature over 10 °C	(Ogawa and Egusa 1978)
Tetraonchus oncorhynchi	Masou salmon		The distal part of filament	Oviparous	-	(Ogawa and Egusa 1978)
Family Diplectanidae						
Diplectanum aequans	Sea bass	Marine waters	Gills	Oviparous	Eggs hatch 2–6 day at 20–30 °C, 7–12 day at 15 °C 11–19 day at 10 °C.	(Cecchini 1994)
Diplectanum laubieri	Sea bass	Marine waters		-	-	(González-Lanza et al. 1991)
Furnestia echeneis	Gilthead sea bream		Gills and inner operculum	-	-	(Paperna and Laurencin 1979)
Family Gyrodactylidae						
Gyrodactylus anguillae	Anguillid eels	Fresh and	Gills, fins, skin, nostrils and pharynx	Viviparous	-	(Ogawa and Hioki 1986)

Table 1 (continued)

Subclasses/family	Host	Macro habitat	Micro habitat	Strategy	Reproductive characteristics and life cycle	Reference
Gyrodactylus salaris	Salmonids	brackish water Freshwater	Fins, skin, cornea and nostrils.	Viviparous	Three generations may be seen in one parasite; can give birth up to 4 times, the time of first birth from 1.8 to 2.3 days depend on host. The second daughter can develop asexually and parthenogenetically, at the same time, this parasite frequently inseminated and third born and subsequent daughter develop sexually (depend on host)	(Cable et al. 2000)
Gyrodactylus derjavini	Salmonids	Freshwater	Skin, fins.	Viviparous	Parasite population reach a peak abundance within 3 weeks at 18.7 °C, 5 weeks at 11.6 °C.	(Buchmann and Uldal 1997)
Gyrodactylus salmonis	Salmonids	Freshwater	Skin, fins buccal cavity and nostrils	Viviparous	-	(Cone and Cusack 1988)
Gyrodactylus katharineri	Common carp and cyprinids.	Freshwater	Skin, fins, gills	Viviparous	Reproduction temperature dependent, 12 °C 64 worms/host on day 27; 99 worms/host on day 16 at 14 °C; and 154 worms/host at 15 days at 18 °C.	(Gelnar 1987)
Gyrodactylus turnbulli	Guppies (*Poecilia reticulata*)	Freshwater	Caudal fins, skin	Viviparous	At 25 °C, worms give birth four times in 1–2-day intervals.	(King and Cable 2007; Richards and Chubb 1996)
Gyrodactylus bullatarudis					Longest life span (5.5 days) at 21 °C, the highest average fecundity (1.73 offspring) at 25.5 °C and the highest instantaneous per capita birth rate (0·543/parasite/day) at 27.5 °C. The intrinsic rate of increase in the parasite population was maximum (0.23 parasite/day) at 27.5 °C. The average fecundity of 1.68 offspring during its expected life span of 4.2 days. The first offspring is born approximately 1 day after the birth of the parent and subsequent offspring are born at 2–2.5-day intervals. The average instantaneous birth rate is 0.43 parasite/day.	(Scott 1982; Scott and Nokes 1984)

Table 1 (continued)

Subclasses/family	Host	Macro habitat	Micro habitat	Strategy	Reproductive characteristics and life cycle	Reference
Gyrodactyloides bychowskii	Atlantic salmon	Marine water	Gills	Viviparous		(Mo and MacKenzie 1991)
Oögyrodactylus farlowellae gen. et sp.nov.	South American loricariid catfish *Farlowella amazonum*	Freshwater		Oviparous	*O. farlowellae* retains eggs individually in the ootype until embryonation. After oviposition, the eggs adhere to the substrate and hatch to give a crawling, unciliated larva. The life cycle (egg to adult) is completed in 11–13 days at 27 °C.	(Harris 1983)
Phanerothecium spinatus sp. n.	Loricariid catfishes	Freshwater		Oviparous		(Boeger et al. 1994)
Hyperopletes malmbergigen. et sp. n.	Loricariid catfishes	Freshwater		Oviparous		(Boeger et al. 1994)
Family Anoplodiscidae						
Anoplodiscus tai	Red sea bream	Marine water	Fins, skin	-		(Ogawa 1994)
Family Microbothriidae						
Dermophthirius nigrellii n. sp	Reef shark	Marine water	Placoid scales	-		(Cheung and Ruggieri 1983)
D. carcharhini	Galapagos shark *Carcharhinus galapagensis*	Marine water				(Rand et al. 1986)
D. penneri	Blacktip sharks (*Carcharhinus limbatus*)	Marine water	Skin			(Bullard et al. 2000)
Family Capsalidae						
Neobenedenia sp.	Not hot specific,	Marine water			Reached sexual maturity at day 10 post-hatch (24 °C, 35‰) and laid ~ 3300 embryonated	(Hoai and Hutson 2014)

Table 1 (continued)

Subclasses/family	Host	Macro habitat	Micro habitat	Strategy	Reproductive characteristics and life cycle	Reference
	more than 100 marine teleost		Skin and eyes, sometimes in gills and nostrils	Oviparous or self-fertilisation	eggs over 17 days. Egg production rapidly increased following sexual maturity on day 10 (58 ± 15 eggs) and peaked on day 15 (496 ± 68 eggs) before gradually decreasing. Laid eggs continuously, but egg production increased in periods of darkness (64.3%), while the majority of oncomiracidia (81%) emerged from eggs in the first three hours of light.	(Deveney et al. 2001; Mueller et al. 1992)
Neobenedenia melleni	Not hot specific, more than 100 marine teleost	Marine water	Skin and eyes, sometimes in gills and nostrils	Oviparous	Eggs are filamented, tanned, operculate and tetrahedral. Egg hatch 5–8 days at room temp.	
Neobenedenia girellae	Major on amberjack and Japanese flounder	Marine water	Body skin and fins in young. Adult on skin, mouth and eye regions.	Oviparous	Reach sexual maturation 15–17 days from the egg, lay 12.2–35.4 eggs/h at 27–30 °C, eggs hatch within 5–6 days at 25 °C. Oncomiracidia first invade fins, post-larval stages on fins before migration to the skin.	(Bondad-Reantaso et al. 1995)
Benedenia monticelli	Mugilid fish	Marine water	Mouth, sometimes in gills and skin	-		(Papema et al. 1984)
Benedenia seriolae	Yellowtail	Marine water	Skin and fins	Oviparous	Egg production is temperature dependent. Larvae may survive up to 1 day. Adult development 2 weeks during the summer season and more than 1.5 months at 17–20 °C. The total life cycle takes 20 days during summer	(Kearn et al. 1992a)
Entobdella soleae	Common sole	Marine water	Skin. migration from the upper part to the lower side of the body for reproduction	Oviparous	Egg development takes 27 days at 13–17 °C. Tetrahedral eggs, adhesive material for attachment to sand grains or other materials in the environment.	(Kearn 1963; Kearn 1974b)

Table 1 (continued)

| Subclasses/family	Host	Macro habitat	Micro habitat	Strategy	Reproductive characteristics and life cycle	Reference
Polyopisthocotyleans						
Family Diclidophoridae						
Heterobothrium okamotoi	Tiger puffer	Marine and brackish waters	Branchial cavity wall, gill filaments	Oviparous	Eggs hatching ranges from 5.3 to 11.8 days (tempt, 15–25 °C). Oncomiracidium could survive much longer than other monogenean larvae (4.7–9.1 days at temperature 15–25 °C)	(Ogawa 1998)
Neoheterobothrium hirame	Japanese flounder	Marine water	Gills	Oviparous (egg attachment at the buccal cavity wall)	Sexual maturity at day 59 at 15 °C, 31 days at 25 °C. 85% eggs can hatch between 10 and 25 °C, < 5% at 30 °C	(Ogawa 1999; Yoshinaga et al. 2000)
Family Discocotylidae						
Discocotyle sagittata	Salmonids: brown trout, rainbow trout	Freshwater	Gills, mainly secondary gill lamellae	Oviparous	Egg hatch within 28 days at 13 °C, oncomiracidia life span is less than 24 h at 13 °C. No transmission occurs during cold winter months.	(Gannicott and Tinsley 1997)
Family Microcotylidae						
Microcotyle sebastis	Rockfish	Marine water	Gills	-	-	(Thoney 1986)
Allobivagina sp.	Siganid fishes	Marine water	Gills	-	-	(Papema et al. 1984)
Heteraxine heterocerca	Japanese yellowtail	Marine water	Gills	Oviparous	Eggs hatched after 5 days at 23 °C, mainly hatched in the dusk and few hours of darkness. Eggs with long filaments entangle in the environment: net meshing in cage culture.	(Kearn et al. 1992b; Mooney et al. 2008)
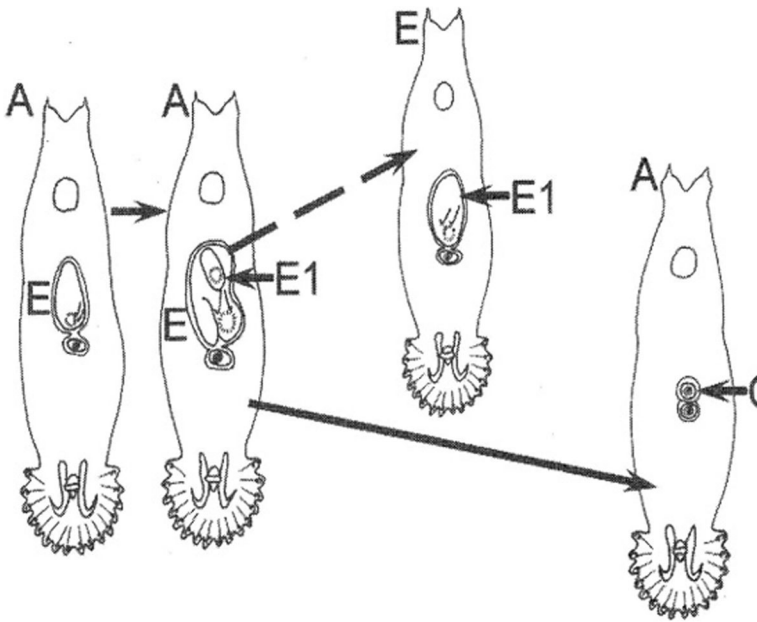
Fig. 5 Viviparity. Diagrammatic representation of viviparity in the Gyrodactylidae. The embryo (E) inside individual (A) grows and develops an embryo inside it (E1). Adapted from Whittington and Chisholm (2008)

(Monogenea: Diclidophoridae) (Ogawa 2002). Furthermore, Ogawa et al.(2014) suggested that self-insemination in *N. girellae* may involve passage of sperm through the tegument from externally attached spermatophores. While the specific mechanism of self-insemination was not determined, Hoai and Hutson (2014) provided the first experimental evidence that a notorious fish monogenean, *Neobenedenia* sp., can produce viable eggs in isolation for three consecutive generations.

Fecundity

Parasites that exhibit high fecundity increase the likelihood of offspring successfully locating and infecting a new host. A large number of eggs can be produced by oviparous monogeneans which hatch into free-swimming larvae (oncomiracidia) and heavy infections can lead to mass mortalities (Buchmann and Bresciani 2006; Whittington and Chisholm 2008). *Neobenedenia* sp., a marine capsalid monogeneans of critical concern to aquaculture, which was demonstrated to produce viable eggs in isolation for three consecutive generations and single worm laid approximately 3300 embryonated eggs over 17 days (Hoai and Hutson 2014). *Neobenedenia girellae* laid a mean of 35.4 eggs/h (Bondad-Reantaso et al. 1995). The daily egg laying rate per worm of *Neoheterobothrium hirame* could reach to 781 eggs at 20 °C (Tsutsumi et al. 2002). *Zeuxapta seriolae* from the gills of yellowtail kingfish (*Seriola lalandi*) in South Australia laid 803 eggs/day. Daily output of the monogenean *Heterobothrium okamotoi* infected tiger puffer throughout the observation period being 51.2–362 egg/parasite. Egg production of *Discocotyle sagittata* (Monogenea) infecting rainbow trout was 12 eggs/worm/day at 18 °C (Gannicott and Tinsley 1998). The capsalid monogenean *Benedenia seriolae*, a skin parasite of the yellowtail, *Seriola quinqueradiata*, laid 27 eggs in 1 h at 20 °C

(Kearn et al. 1992a). Egg production in the monogenean *Entobdella soleae* increases as adult parasites grow and can reach 60 eggs per day (Kearn 1985). Therefore, the knowledge of specific species' reproductive biology is crucial to inform integrated strategic parasite management in aquaculture.

For viviparous monogeneans, Gyrodactylids represent one of the most diverse and widespread taxons of mongenoidea with *Gyrodactylus* including 402 species worldwide and parasizing fishes representing 19 teleost orders (Bakke et al. 2002). Although study on the reproduction of viviparous parasites are inadequate, a study demonstrated that during live cycle of the viviparous ectoparasite, *Gyrodactylus bullatarudis*, infecting reared guppies (*Poecilia reticulata*), three generations may be represented in one worm and the first daughter can be born within 24 h of the birth of the parent, and six million offspring can be produced in just 4 weeks from the parent (Scott 1982). Moreover, viviparous *Gyrodactylids* are found in freshwater, brackish water and marine environments and also occur on some cephalopods, crustaceans and amphibians. Therefore, reproduction strategies of viviparous parasites may extremely varies.

Egg morphology and distribution

Egg morphology from the diversity of oviparous monogeneans differs considerably between species. Eggs can be spherical, oval, ovoid, prolate spheroids, fusiform or tetrahedral. For instance, *Benedenia* sp. and *Neobenedenia* sp. produce tetrahedral eggs bearing long filamentous threads 2–4 mm (Kearn et al. 1992b). Eggs are non-motile and follow diffusion laws. However, the filamentous thread may easily to attach to substrate in aquaria or aquatic habitats (Deveney et al. 2001; Ernst and Whittington 1996). Other species, such as *Heterobothrium okamotoi* and *Neoheterobothrium hirame*, tend to produce eggs with short or long extensions (Ogawa 2011). Eggs may be laid singly or may be tethered together in bundles, strings or chains (Kearn 1986; Ogawa 2002; Ogawa et al. 2005; Whittington and Kearn 1988). In most species, eggs will embryonate and hatch releasing ciliated larvae while others release nonciliated (MacDonald and Llewellyn 1980).

Although most adult monogeneans tend to shed their eggs directly into the water column, there are some rare exceptions in which parasites and eggs have special strategies or characteristics to enhance survival (Whittington 2005). For instance, adult *Acanthocotyle* retains their eggs outside the body until they hatch, while a new *Benedenia* Species (Monogenea: Capsalidae) from *Diagramma labiosum* (Perciformes: Haemulidae) attaches its eggs to host tissue (Whittington and Deveney 2011). *Monocotyle multiparous* can store eggs inside its body until the eggs hatch internally (Whittington and Chisholm 2008).

Egg laying rhythms

Parasite egg–laying rhythms could be predator avoidance behaviour and could also align with temporal host behaviours. The egg laying rhythm of *Diplozoon homoion gracile* (Monogenea: Diplozoidae), a gill parasite of southern barbel, *Barbus meridionalis*, is also nocturnal (Macdonald and Jones 1978). Similarly, Mooney et al. (2008) found that *Heteraxine heterocerca* (Monogenea: Heteraxinidae) a gill parasite of Japanese yellowtail, *Seriola quinqueradiata*, laid eggs continuously, but more eggs (72.9%) were laid during periods of

darkness, with the majority of eggs released during the first 3-h periods immediately after dark. Alternatively, some monogenean species store their eggs in utero until releasing at a specific time of day (Mooney et al. 2006, 2008; Poddubnaya et al. 2017; Tinsley 2017). *Neobenedenia* sp. laid eggs continuously, but egg production increased in periods of darkness (64.3%) (Hoai and Hutson 2014).

Egg hatching strategies

The free-swimming monogenean larvae phase (larvae = oncomiracidia) are typically short lived (24 to 48 h) (Militz et al. 2014; Whittington and Chisholm 2008; Whittington and Kearn 2011), and normally less than 24 h at higher temperatures (Buchmann and Bresciani 2006; Glennon et al. 2006), excepted for *Heterobothrium okamotoi* larvae (4–9 days) (Ogawa 1998). Larvae that successfully locate a host will attach and shed their ciliated cells, whereupon they develop into the adult stage. Swimming speed of most ciliated larvae is approximately 4 mm/s, and they display specific behaviours such as phototaxis, geotaxis, rheotaxis and chemotaxis (Whittington et al. 1999). Hatching rhythms are crucial for infection success because this could increase the chances of larvae contacting a specific host in situation of short-time survival, environmental condition which is related to host behaviour and physiology can also contribute to hatching strategies of monogenean eggs (Ernst and Whittington 1996; Whittington and Ernst 2002). Different egg hatching strategies, such as spontaneous hatching, major hatching in darkness or major hatching in light, have been identified in several studies. For example, Whittington and Kearn (1986) found that eggs of *Rajonchocotyle emarginata* from the gills of *Raja* spp. (Rajidae) hatch spontaneously. The majority of oncomiracidia (81%) emerged from eggs of *Neobenedenia* sp. in the first 3 h of light (Hoai and Hutson 2014). *Discocotyle sagittata* displays a clearly defined nocturnal egg hatching rhythm and incubated eggs in alternating 12-h periods of light and darkness at 13 °C hatched mainly within the first 2 h of darkness (Whittington 1987). Host behaviour and physiology may also have a vital role in the egg hatching process. For example, mucus extract from fish hosts has been observed to act as an effective hatching stimulus for several species (Kearn 1974b; Macdonald 1974). Kearn (1973) had investigated that embryonated eggs of the sole skin parasite *Entobdella soleae* exposed to an artificial day/night cycle fully embryonated egg will hatch spontaneously but larvae emerged in pulses, not continuously, corresponding to the first 2 or 3 h after 'dawn' on each day. This periodicity is significant because sole (*Solea solea*) is nocturnally active, feeding mainly on bottom-dwelling polychaetes, and spending most daylight hours partly buried in sediment. *Hexabothrium appendiculatum*, which infects *Scyliorhinus canicula* (Scyliorhinidae), hatch only under the stimulation of host skin secretions (Whittington 1987). Similarly, *Squalonchocotyle torpedinis* from *Torpedo marmorata* (Torpedinidae) hatches in the presence of host gill tissue (Euzet and Raibaut 1960; Glennon et al. 2006). However, the egg of *Neonchocotyle pastinacae* from the gills of *Dasyatis pastinaca* (Dasyatidae) hatches only when mechanically disturbed (Ktari and Maillard 1972). It is generally assumed that hatching rhythms of monogeneans have adaptive value related to host behaviour. However, in some case, it has been demonstrated that predation on monogenean larvae, especially by filter-feeding invertebrates, may also influence the time of hatching (Ernst and Whittington 1996; Whittington and Kearn 1986).

Factors affected on live cycle of monogeneans

For many monogenean species, reproductive biology parameters are poorly studied or completely unknown. Compounding this is the huge diversity of monogeneans and their various reproductive strategies, so it is difficult to make generalisations representative of the majority of monogenean species and their host interactions (Whittington and Chisholm 2008). For most monogeneans, the rate of development (embryonation period, larva longevity, age at sexual maturity and adult life span) is influenced by environmental factors such as water temperature, light intensity and salinity or host species (Bauer et al. 1973; Buchmann and Bresciani 2006; Gannicott and Tinsley 1997).

Temperature

Low water temperatures result in slow development of eggs and parasites than that at higher temperatures. For example, Cone and Burt (1981) demonstrated that *Urocleidus adspectus* (Monopisthocotylea) is unable to lay eggs at 4 °C, and larvae are mostly absent in winter fish samples of the host fish, yellow perch. However, when water temperature increased seasonally, egg laying activities resumed. Hirazawa et al. (2010) found that the life span of *Neobenedenia girellae* after larvae attachment to the host amberjack *Seriola dumerili* (Carangidae) was shorter at increased water temperatures. Water temperatures also strongly influence egg development, which can impact the time taken for a monogenean to complete its life cycle. In an investigation by Ernst et al. (2005), egg embryonation period of *Benedenia* sp. was 5 days at 28 °C and 16 days at 14 °C. Similarly, for *B. seriolae* infecting *Seriola lalandi* in New Zealand, egg hatching peaked at 22, 11 and 9 days at 13, 17.5 and 21 °C, respectively. Therefore, egg embryonation period is shorter for these parasite species in warmer water temperatures. Age at sexual maturity is also highly influenced by the water temperature and may differ between host species and locality. In general, parasites often reach sexual maturity earlier at higher temperatures. For example, Tubbs et al. (2005) reported that *B. seriolae* attained sexual maturity at 48, 25 and 20 days at 13, 18 and 21 °C, respectively, on *S. lalandi*. Brazenor and Hutson (2015) demonstrated that the life cycle of *Neobenedenia* sp. was faster in warm conditions compared with cooler conditions (10–13 days at 26–32 °C compared with 15–16 days at 22–24 °C).

Light intensity

Light intensity is one of the factors influence the egg hatching process, creating hatching rhythms which may increase the chances of larvae contacting a specific host and minimise predation on monogeneans by other organisms, especially filter feeders (Euzet and Raibaut 1960; Kearn 1974a). This is crucial for infection success because free-swimming oncomiracidia are typically short lived (24 to 48 h); thus, hatching rhythms could maximise their chances of finding a host (Tsutsumi et al. 2002; Ktari and Maillard 1972). Kearn (1963) reported that *Entobdella soleae* egg hatching is stimulated by illumination after a period of darkness. Similarly, rapid hatching of eggs lay from the monogenean *Entobdella diadema* was found to induce by light intensity reduction (Kearn 1982). The eggs of the polyopisthocotylean monogenean *Plectanocotyle gurnardi* Llewellyn from the gills of gurnards (Triglidae) develop and hatch readily might be the consequence of inadvertent shadowing (Whittington and Kearn 1989). Gannicott and Tinsley (1997) observed the egg hatching in the monogenean gill

parasite *Discocotyle sagittata* from the rainbow trout (*Oncorhynchus mykiss*) revealed that *Discocotyle sagittata* displays a clearly defined nocturnal egg hatching rhythm and the majority of larvae hatched within the first 2 h of darkness. Mooney et al. (2008) also reported that 45.4 % of egg production of *Heteraxine heterocerca* and *Benedenia seriolae* occurred during the first 3-h period following darkness. In contract, hatching rhythms have been documented in other marine monogeneans in the first few hours of light such as *Entobdella solea* (Kearn 1973), *Diclidophora* spp. (Macdonald 1975) and *Neobenedenia* sp. (Hoai and Hutson 2014). Other species exhibit more complicated rhythms (see Macdonald and Jones 1978; Euzet and Raibaut 1960; Hirazawa et al. 2010; Ernst et al. 2005).

Salinity

The influence of salinity on hatching rate and larval development of a variety of monogenean parasites has also been investigated. Salinities higher than 50‰ and lower than 15‰ result in limited or no egg hatching for marine monogeneans (Ernst et al. 2005). Salinities between 0 and 5‰ caused 100% embryo mortality in the microcotylid *Polylabroides multispinosuss*, although no mortality was observed between 10 and 20‰ salinity (Diggles et al. 1993). The decreases of salinity reduced hatching success and retarded larval development and low salinities (0–6.7 ppt) were obviously affected to development of embryos of *Heterobothrium okamotoi* and *Heterobothrium ecuadori*, often resulted in apparently inactive or no hatching of eggs, while the hatching time ranged from 7 to 10 days in standard seawater conditions (35‰ salinity) at 23 ± 1 °C for *Heterobothrium ecuadori* (Grano-Maldonado et al. 2015; Ogawa 1998). Some other studies have reported that egg hatching is disrupted in 0‰ salinity for a number of monogenean species (Balasuriya and Leong 1995; Diggles et al. 1993; Mueller et al. 1992). The egg hatching rates for the monogenean *Neobenedenia girellae* at 8‰ and 17‰ salinity were found to be significantly lower than that observed at 34‰ salinity (Umeda and Hirazawa 2004). Brazenor and Hutson (2015) demonstrated that Warm seawater and high saline conditions (24–32 °C, 35–40‰) improved egg hatching success, reduced time to sexual maturity and resulted in parasites reaching sexual maturity at a larger size (at 30–32 °C) compared with cooler conditions (22 °C). In contrast, cool, hypersaline conditions (22 °C, 40‰) increased oncomiracidia longevity and infection success. Experiments with the oncomiracidia of the *diclidophorid Diclidophora denticulata* demonstrated that exposure to low salinity resulted in slowed movements after 15 min and death after 1 h (Frankland 1955). Exposure of the oncomiracidia of *H. okamotoi* to 0‰ salinity for 20 min resulted in death (Ogawa 1998). These results suggest a lack of osmoregulation capability in this ciliated larva, which is consistent with an organism's survival depending on the biology of the species or environmental variables (Ernst et al. 2005; Shirakashi et al. 2010). Although the free-swimming period is usually short, further studies on swimming activity are essential to determine the factors responsible for interfering with this mechanism in low-salinity environments. Typically, a 40–50 ppt saltwater bath or freshwater bath for approximately 5 min is used to rid marine fish of attached monogeneans (Thoney and Hargis 1991).

Host species

In addition, several studies have demonstrated that the rate development of parasites can be different between host species, influencing generation time, age at sexual maturity as well as size of the adult parasite. For example, Hirayama et al. (2009) reported that *Neobenedenia*

girellae grow and reach sexual maturity faster on amberjack *Seriola dumerili* compared with yellowtail *Seriola quinqueradiata* or *Paralichthys olivaceus*. As a result, a relatively larger number of eggs are laid by parasites infecting *S. dumerili* (Ohno et al. 2009). Furthermore, while Kearn et al. (1992b) reported that *B. seriolae* reached sexual maturity on yellowtail *Seriola quinqueradiata* after 14 days at 22 °C, Tubbs et al. (2005) found parasites were reaching maturity at 20 days at 21 °C on *S. lalandi* in New Zealand. These studies demonstrate that generation time of monogeneans may differ in different environmental conditions, hosts and localities.

Treatments of monogeneans

Limited knowledge on the reproductive strategies of Monogeneas is a considerable barrier for disease protection. The effects of water conditions on each phase in the life cycle result in many challenges for management of monogenean outbreaks. There are no methods to prevent monogenean infections; most allow only temporary respite by removing parasites, and none provide any protection against immediate reinfection (Whittington 2012). Culture activities in aquaculture may have a vital role in whether the disease outbreaks occur because stressed fish tend to have lowered resistance to monogenean infections (Whittington and Chisholm 2008). As a result, reducing stressors to fish such as reducing stocking densities and ensuring good water quality should be initial steps to manage monogenean proliferation. Potential treatment methods for fish infected by monogeneans can be divided into four major groups including mechanical, biological, chemical and eggs treatments (Cowell et al. 1993; Do Thi Hoa 2007; Whittington 2012).

Mechanical control

Removing eggs from culture systems could effectively reduce infections. This can potentially be achieved by filtration of inflow and outflow water in recirculation systems (Whittington and Chisholm 2008). Regular cleaning or replacement of badly fouled sea cages may also significantly reduce the number of monogenean eggs retained in the system (Ernst and Whittington 1996; Glennon et al. 2006). However, frequent net changes may not be feasible in all circumstances and the rapid development of eggs in high temperatures may lead to rapid recontamination of a location in a short time (Ernst and Whittington 1996; Ernst et al. 2005; Lin et al. 2008). Reducing egg loads by placing additional fouling substrates within sea cages and removing them prior to hatching may alleviate the number of larvae in systems (Ogawa 2002; Ogawa et al. 2006). However, the effectiveness of this approach has not been examined. This practice could perform in experimental work or closed systems, but maybe impractical on a commercial scale.

Biological control

Biological control of monogeneans using cleaner organisms could be a cost-effective alternative compared with labour-intensive management methods (Cowell et al. 1993; Whittington and Chisholm 2008). Cleaner fish species are not particularly selective in their food choice, and they readily ingest both adult and larval monogeneans (Buchmann and Bresciani 2006). Various examples using cleaner fish to reduce the effects of monogeneans in aquaculture have been reported (Grutter et al. 2002; Militz and Hutson 2015; Vaughan et al. 2017). For instance,

the cleaning goby, *Gobiosoma genie*, significantly reduced infections of *Neobenedenia melleni* on cultured Florida red tilapia (Cowell et al. 1993). Grutter et al. (2002) subjected the capsalid monogenean, *Benedenia lolo*, infecting skin of the thick-lipped wrasse (*Hemigymnus melapterus*) to predation by the cleaner fish *Labroides dimidiatus*. These authors found that cleaner fish selectively removed larger monogeneans. Copepods and other crustaceans can also reduce monogenean populations by feeding on oncomiracidia in recirculating systems (Buchmann and Bresciani 2006). Militz and Hutson (2015) demonstrated that cleaner shrimp, *Lysmata amboinensis*, consume eggs and larvae of a harmful monogenean parasite, *Neobenedenia* sp., in aquaculture. For example, shrimp consumed parasite eggs under diurnal (63%) and nocturnal (14%) conditions as well as infectious larvae (oncomiracidia) diurnally (26%). The cleaner shrimp also reduced oncomiracidia infection success of host fish by half compared with controls.

Chemical control

Chemical treatments can only provide short-term control as they are only effective on attached parasites stages (Ernst et al. 2005). As a result, coordinated treatments are required to prevent fecund adult parasites recontaminating an area following an initial treatment. Otherwise, the untreated eggs and larvae can rapidly reinfect treated fish, resulting in continuous cycles of treatment (Ernst et al. 2005). Understanding the parasite's life cycle parameters and the influences from environmental factors improves the effectiveness of disease management.

Numerous chemicals have been trialled to manage monogenean infections with varying success. The most widely used are copper sulphate, formaldehyde, sodium chloride, hydrogen peroxide and other oral treatments (Buchmann and Kristensson 2003; Chisholm and Whittington 2002; Ellis and Watanabe 1993; Janse and Borgsteede 2003; Kim and Choi 1998; Rach et al. 2000). However, the most important consideration when using chemicals is the toxicity to the host and the parasite which is dependent on the species as well as biotic and abiotic conditions (Woo 2006). Therefore, extreme caution must be taken and each parasite-host system should be examined specifically prior to using a treatment on a large scale.

Formalin is a widely applied and effective method to remove monogeneans from fish skin, gills and tanks in closed systems. The applied concentrations vary between 25-500 ppm depending on the duration of treatment (Thoney and Hargis 1991). It can be used to bath fish for a short time at high concentrations (30-100 ppm) or at low concentrations (25-60 ppm) for extended periods. However, the use of formalin must be considered carefully because it can be stressful to fish and harmful to humans.

Hydrogen peroxide is a strong oxidizing agent which is used in bathing treatments to effectively eliminate monogeneans (Rach et al. 1997). Various concentrations and treatment durations have been practiced in the management of monogeneans in aquaculture (Table 2). This chemical has no food safety issues and has been approved for use as a bath treatment in several countries. Hydrogen peroxide can also be administered in the form of sodium percarbonate, where hydrogen peroxide is released more slowly and has a prolonged action in the water. However, high concentrations of hydrogen peroxide can be toxic to fish (Hirazawa et al. 2017; Roque et al. 2010). As a result, treatment duration and concentration should be tested carefully (Kiemer and Black 1997). Furthermore, depending on season and temperature, the toxicity of hydrogen peroxide can be varied. Rach et al. (1997) demonstrated that toxicity of hydrogen peroxide is higher at higher temperatures and suggested that fish farms should supply additional oxygenation when treating in summer to reduce fish mortality.

Table 2 Hydrogen peroxide treatment for monogenean infection

Concentrations	Treatment duration	Parasites/host	Effectiveness	References
< 560 mg/l	30 min every 2 days	*Gyrodactylus* (Monopisthocotylea)/rainbow trout	Removes all parasites	(Rach et al. 2000)
80 ml/l	18 h	*G. derjavini*/rainbow trout	Removes all parasites	(Buchmann and Kristensson 2003)
300 ppm	10 min	*Zeuxapta seriolae* (Polyopisthocotylea)/yellowtail kingfish	Removes all parasites	(Mansell et al. 2005)
50 mg/l	2–7 days	*Gyrodactylus salmonis*/rainbow trout	99% reduction of parasites	(Bowker et al. 2012)
570 mg/l	4 min	*Ligictaluridus floridanus*/catfish (*Ictalurus punctatus*, Rafinesque)	Removes all parasites	(Benavides-González et al. 2015)
75 ppm	30 min	Benedenia seriolae, Neobenedenia girellae, Zeuxapta japonica/amberjack (*Seriola dumerili*)	Removes all parasites	(Hirazawa et al. 2016)

Mebendazole and praziquantel are two main drugs widely used to treat diseases caused by monogeneans. Mebendazole-based compounds bind to tubulin monomers in the parasite to destroy microtubules in cytoskeletons and cell transport functions (Buchmann and Bresciani 2006; Whittington and Chisholm 2008). This chemical group, including albendazole, fenbendazole, flubendazole, luxabendazonle, mebendazole, oxfendazole, parbendazole, tricladbendazole and thiabendazole, has been trialled in previous studies to against monogeneans. Mebendazole was first used by Goven and Amend (1982) to treat *Gyrodactylus elegans* from goldfish, in which a 24-h treatment of 0.01 mg/l mebendazole effectively removed all attached parasites. Buchmann and Bjerregaard (1990) also used this drug at 1 ppm to bath the European eel, *Anguilla anguilla*, infected with *Pseudodactylogyrus bini* within 72 h of treatment, infections were effectively eradicated. However, some parasite species are not affected by this chemical (Katharios et al. 2006) and the dosage required to effectively treat against a wide range of parasites is unknown (Whittington and Chisholm 2008). In addition, studies were also indicated that after prolonged exposure, monogeneans become resistant to mebendazole (Buchmann et al. 1992) and caused gill injury for fish (Führ et al. 2012). Praziquantel is a drug of choice in the control of schistosome and cestode infections in humans and animals. And in the 1970s, it was demonstrated to be effective in eradicating monogeneans on fish. As a result, this drug has wide application against monogeneans by bathing fish and also in oral treatments in marine and freshwater fish culture (Table 3).

Egg treatments

The biological and chemical treatments presented above are largely focused on killing adult parasites and there is limited information on treatments that effectively kill eggs. Several experiments have been conducted successfully to treat eggs of monogeneans (Fajer-Avila et al. 2007; Umeda et al. 2006). However, it is difficult to apply into field because the accumulation and distribution of monogenean eggs in ponds, cage culture, was overestimated and could not

Table 3 Praziquantel treatments for monogeneans

Host	Parasite	Treatment method dosage/ duration	Effectiveness	Reference
Teleosts and elasmobranchs	'Skin' parasites	Bath; 10–20 mg/l; 1–3 h	Remove pathogens	(Thoney 1990; Thoney and Hargis 1991)
Rockfish	*Microcotyle sebastis*	Bath 100 ppm for 4 min	Remove all specimens	(Kim and Cho 2000)
The Rhinobatos typus	Monogenean	Bath; 5 mg/l; 40 h	Remove all gill and nasal monogeneans	(Chisholm and Whittington 2002)
Yellowtail kingfish	*Benedenia seriolae* and *Zeuxapta seriolae*	Bath, 2.5 ppm, 24–48 h	Remove all parasites	(Sharp et al. 2004)
	Benedenia seriolae and *Zeuxapta seriolae*	70 mg kg^{-1} BW for 3 days	81.6 and 99.4 % efficacy, respectively	(Forwood et al. 2016)
Rockfish	*Microcotyle sebastis*	Oral 200 mg/kg BW	Lowered	(Kim et al. 1998)
Rockfish	*Microcotyle sebastis*	Oral; combination of praziquantel and cimetidine; 200 mg/kg	Increase ability against monogeneans	(Kim et al. 2001)
Spotted eagle ray	*Dendromonocotyle torosa*	Oral 10–40 mg/kg BM	No effect	(Janse and Borgsteede 2003)
	Clemacotyle australis	25 mg/l bath	Remove all parasites	(Janse and Borgsteede 2003)
Silver perch *Bidyanus bidyanus* (Mitchell)	*Lepidotrema bidyana* Murray	Oral 10 mg/l for 48 h 75 mg/ kg	99% efficacy 79% efficacy	(Forwood et al. 2013)
Spotted halibut Verasper variegatus (Pleuronectidae)		40 mg/kg BW/day for 11 days	Significant reduce parasites	(Hirazawa et al. 2004)

control (Shirakashi and Hirano 2015). In addition, Sharp et al. (2004) and Ernst et al. (2005) demonstrated that desiccation for 3 min to 3 h is an effective method to prevent egg hatching, but this strategy is only feasible in closed facilities and ponds that can be dried out over extended periods.

Conclusion

Monogeneans are flatworms (Platyhelminthes) with representatives in freshwater, brackish and marine habitats. Monogeneas are also highly diverse, and the vast majority of species are ectoparasitic. They all have a direct life cycle with a variety of reproductive strategies including oviparity, viviparity and self-fertilisation. These are a prerequisite for the fast development of outbreaks. Monogenean biology such as reproduction, generation time, fecundity and egg laying patterns are mostly unknown or limited and become the knowledge gap and challenges to control and manage this disease in wild and farmed fish. Consequently, the severe impact of monogeneans in both cultured and wild fish populations are apparent and need more attention to

mitigate the outbreaks and economic loss. Chemical and drug control efforts have been widely used. However, due to chemical and drug legislation and also their environmentally unfriendly effects, many of these are not allowed in many countries. Thus, integrated control should be encouraged to prevent monogenean outbreaks using feasible methods such as mechanical removal of eggs and larvae by filtration, reducing entrapment of eggs and larvae in a stationary production system and using of cleaner fish prior to finally using strategic treatments with chemicals or anthelmintics.

Future research efforts would be best to focus on the fundamental biology of these fascinating parasites using live specimens on live hosts. These will assist in revealing data of intrinsic value to fill up the knowledge gap and also provide critical suggestions for effective and efficient parasite management in aquaculture. Effective surveys and actions to prevent introduction of monogeneans into new host populations, the ecological and physiological studies on the parasite and host-parasite interactions may both contribute to providing new ways to control diseases caused by monogeneans in the future. Finally, antiparasitic control programmes should be encouraged and funding provided to find out new effective and environmentally friendly solutions to prevent the disease outbreaks caused by parasitic flatworms.

Compliance with ethical standards

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

Ethical approval   This article does not contain any studies with animals performed by anyof the authors.

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