

# Revisiting cannibalism in fishes

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**Abstract** Cannibalism, the act of eating an individual of the same species, has long intrigued researchers. More than 30 years after publication of reviews on the topic, there appears to be little consensus about the commonness of cannibalism and its ecological and evolutionary importance. Since Smith and Reay (Rev Fish Biol Fish 1:41–64, 1991. doi:10.1007/BF00042661) reviewed cannibalism in teleost fish, many new studies have been published that address aspects of cannibalism and here we present an updated review. Reports of cannibalism have increased, especially since the 1990s, with many accounts from aquaculture research. Cannibalism has been recorded for 390 teleost species from 104 families, with 150 species accounts based only on captive fish. The number of literature reports of cannibalism is almost equal for marine and freshwater fishes; freshwater families with most reported cases are Percidae, Salmonidae and Esocidae, and marine families are

Gobiidae, Gadidae and Merlucciidae. Ecological and evolutionary implications of cannibalism are discussed along with perspectives for future research.

**Keywords** Aquaculture · Feeding · Intraspecific predation · Literature survey · Reproduction

## Introduction

In his classic book *The Selfish Gene*, Dawkins (1976) proposed that cannibalism, the consumption of conspecifics, should be rare. His logic was that the fitness advantage of gaining nutrition while eliminating potential competitors is unlikely to exceed the fitness disadvantage posed by increased risk of predation mortality for progeny and other closely related individuals (Dawkins 1976). However, based on a literature review, Polis (1981) asked “Why cannibalism is relatively common?” He noted that cannibalism can influence population structure because it generally involves individuals of different sizes (asymmetric relationship) rather than similar sizes (symmetric relationship) as supposed by Dawkins (1976). More than 30 years after Polis’s review, there appears to be little consensus about the commonness of cannibalism and its ecological and evolutionary importance.

Cannibalism, defined more specifically as the act of eating all or part of an individual of the same species irrespective to its development stage (Smith and Reay 1991), has long intrigued fish biologists. In 1852,

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Hancock, reported a case of cannibalism by three-spine sticklebacks (*Gasterosteus aculeatus*, Gasterosteidae) in which a nesting adult consumed a juvenile that had approached it from another nest. Several papers from the early 1900s contain reports of cannibalism among salmonids (e.g., Henshall 1902; Stranahan 1903; Titcomb 1905; Johnson 1906; Stranahan 1912), *Fundulus heteroclitus* (Newman 1907), *Perca fluviatilis* (Allen 1935) and *Esox lucius* (Wurtz 1944). In a classic paper entitled “*Stock and Recruitment*”, Ricker (1954) emphasized the role of cannibalism as a density-dependent regulator of fish populations. Ricker’s paper is credited with being the first to discuss the ecological significance of cannibalism (Smith and Reay 1991). Density regulation from cannibalism has been demonstrated in experiments with live-bearing fish (*Poecilia* spp.) (Thibault 1974; Jones et al. 1998; Riesch et al. 2012; Barki et al. 2013a, b; Nilsson and Persson 2013); however, its importance for regulation of natural populations remains unknown (Smith and Reay 1991). Few studies report cannibalism among wild poeciliids, and when reported, the frequency is very low (Nesbit and Meffe 1993; Ivantsoff 1999; Specziár 2004).

Reviews by Fox (1975a) and Polis (1981) discussed several aspects of cannibalism, and Smith and Reay (1991) were the first to review cannibalism in teleost fishes. Smith and Reay concluded that cannibalism is common among teleosts and discussed some of its causes and consequences. Several subsequent studies focused on specific aspects of cannibalism in fish, including its occurrence during reproduction (Manica 2002) and in aquaculture (Hecht and Pienaar 1993; Baras and Jobling 2002), dietary contribution (Juanes 2003), and evolutionary aspects (Nishimura and Isoda 2004). Additionally, some books and book chapters have addressed aspects of cannibalism (e.g., Elgar and Crespi 1992; Folkvord 1997; Baras 2013). The present review is based on an extensive literature search that updates and expands Smith and Reay’s analysis of cannibalism in teleosts, and also explores some new topics that merit investigation.

## Methodology

A literature survey was conducted using the *Web of Science* database (ISI—Institute of Scientific Information; access: <http://apps.webofknowledge.com>)

and the keywords “fish” and “cannibalism” with November 2015 as the final date. Because many cases of cannibalism are recorded during dietary studies or during research on captive animals (Smith and Reay 1991), a second search with the keywords “trophic ecology of fish”, refined by the word “feeding” also was performed using the same database. Duplicate results and publications that did not report original accounts (e.g., modeling studies, isotopic analyses, or reviews) were excluded. For publications reporting cannibalism, the following information was obtained: (i) publication year, (ii) environment (freshwater or marine), (iii) taxonomy, (iv) natural feeding habit of the cannibal species during the adult stage, (v) observations made in nature versus captive setting (laboratory or aquaculture), (vi) classification of cannibalism type, and (vii) cannibalism frequency reported for fish in natural habitats.

Classification of cannibalism was done by three criteria proposed by Smith and Reay (1991): (i) developmental stage of the prey (e.g., egg, larva, juvenile), (ii) genetic relationship of cannibal to prey (filial cannibalism—parents eating its own offspring, sibling cannibalism—predation of one sibling on another, or non-kin cannibalism—cannibalism between unrelated individuals), and (iii) age relationship of cannibal and prey (intra- vs. inter-cohort). The term “juvenile” here refers to small, pre-reproductive individuals. We also recorded any reported information about the predator’s sex and quantities of eggs consumed from spawned clutches. Many fishes exhibit aggression towards conspecifics, which can be a precursor of cannibalism. However, mortality caused by injuries from attacks by conspecifics without subsequent ingestion of the injured fish is not considered cannibalism (Hecht and Pienaar 1993). Because every study did not report all types of information, our database is asymmetrical and contains gaps. Although our literature search did not include grey literature (e.g., theses, conference proceedings) and probably missed accounts within books, this review nonetheless provides broad assessment that should be representative of current evidence.

Cannibalism frequency was calculated as the proportion of cannibals reported among the total number of individuals observed or analyzed in a given study. In dietary studies, this proportion was based on the number of stomachs examined; for reproduction studies, this was based the number of individuals

observed. Several studies did not report the number of stomachs analyzed or individuals observed, and therefore cannibalism frequencies could not be estimated. Cannibalism frequency values were arbitrarily classified as rare (value < 5%), low (5% < value < 25%), frequent (25% < value < 75%) and high (value > 75%).

Feeding habits were classified based on information provided in the original publications; when this information was lacking, categorizations in *FishBase* (Froese and Pauly 2015) were adopted. Because the dataset includes publications dating back to 1939, *FishBase* was consulted to update fish taxonomy.

#### Literature search results

The literature survey yielded more than 1000 publications reporting cannibalism in teleosts, with more than 80% of papers published after 1990. Smith and Reay (1991) reported cannibalism for 36 teleost families distributed in 106 species, and the present study expands this list to 104 families and 390 species, of which 150 are based only on reports for captive fish. Most reports of cannibalism in nature were based on dietary analysis without details regarding behavior. Direct observations of cannibalism were from research in aquaculture, field studies of reproductive behavior, and lab studies with captive fish. Some recent studies of trophic ecology employed new techniques that improve resolution, such as DNA analysis of gut contents (Rosel and Kocher 2002; Barnett et al. 2010; Eigaard et al. 2014; Jo et al. 2014; Paquin et al. 2014). The greater number of accounts of fish cannibalism reported in recent literature could be due, in part, to electronic archiving of studies published after 1990 and incomplete digital archives for earlier publications.

Studies investigating cannibalism in nature appear to be uncommon, and most field reports of cannibalism were associated with studies of community trophic ecology and not directly focused on cannibalism. Most species with high rates of cannibalism reported from captive settings reveal little to no cannibalism in natural habitats (Fuentes and Quiroga 2012). For example, captive dorada (*Brycon moorei*, Bryconidae) cannibalized early life stages (Baras et al. 2000b), but cannibalism has not been reported from dietary studies of wild populations.

The number of literature reports of cannibalism was almost equal for marine and freshwater fishes. Many fish species cannibalize early development stages. Species

from the marine families Apogonidae, Gobiidae and Pomacentridae are primarily egg predators, usually involving filial cannibalism by nesting species. Anchovies (Engraulidae) and other planktivorous fishes sometimes consume eggs of conspecifics, and presumably, most of them are unrelated. Species of Bryconidae, Cyprinidae, Pimelodidae, Poeciliidae (freshwater families) and Serranidae (marine) feed almost exclusively on larval stages, and Merlucciidae (marine) and Salmonidae (freshwater and anadromous) feed mostly on juveniles. Cannibalism accounts were dominated by a few freshwater families: Percidae (140 occurrences, with *Perca fluviatilis* and *P. flavescens* most frequent), Salmonidae (75 occurrences, with *Salvelinus alpinus* most frequent) and Esocidae (54 occurrences, with *Esox lucius* most frequent) and marine families Gadidae (106 occurrences, with *Gadus morhua* most frequent), Gobiidae (54 occurrences with *Pomatoschistus microps* most frequent) and Merlucciidae (29 occurrences, with the genus *Merluccius* most frequent) (data summary appears in Appendix of supplementary material). Some publications report cannibalism for more than one species; therefore, total cannibalism occurrences exceed the number of publications.

#### Feeding habits

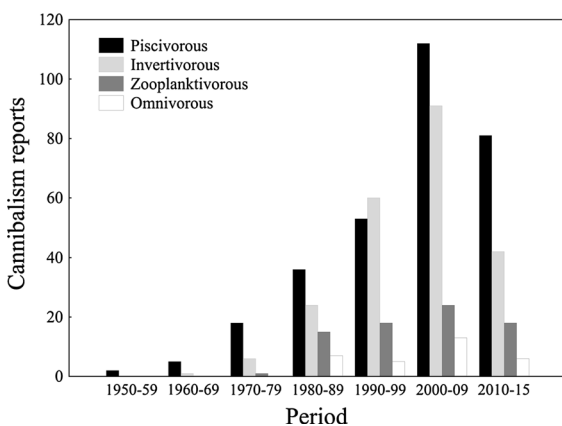
Smith and Reay (1991) noted that cannibalism is most common among piscivorous fishes. According to the present review, cannibalism is most frequently observed among carnivorous fishes, especially those with diets containing various proportions of aquatic insects, crustaceans, mollusks and fish. Many freshwater fishes that feed mostly on benthic invertebrates have frequencies of cannibalism almost as high as those reported for piscivores. Some carnivorous fish switch between feeding on fish and invertebrate prey depending on relative prey availability (Svenning and Borgström 2005; Venturelli and Tonn 2006; Berg et al. 2010; Yağcı et al. 2014), and cannibalism may result from high conspecific density in combination with low prey diversity and abundance. Cannibalism by non-carnivorous species, e.g., those that feed on algae, plants and/or detritus, was rarely reported in nature, and three cases of partial filial cannibalism were reported for two herbivorous pomacentrids (Petersen 1990) and one detritivorous gobiid (Hernaman et al. 2009).

Cannibalism is usually observed in piscivores because members of this guild have enhanced abilities

for detection and capture of fish prey (Smith and Reay 1991). Most piscivorous fishes are invertivorous during early life stages, with infrequent reports of cannibalism among their larvae (e.g., Prado et al. 2006). In contrast, certain herbivorous species, such as *Brycon* spp. (Bryconidae) and *Colossoma* spp. (Serrasalminidae), that feed on fruits have carnivorous larvae that normally feed on tiny invertebrates but sometimes exhibit cannibalism in aquaculture settings (Baras et al. 2000a, b; Liao et al. 2001). These observations suggest that cannibalism is a species-specific trait rather than a general behavioral strategy that depends on certain environmental conditions. The greater number of recent accounts of cannibalism among non-piscivorous trophic guilds could be a function of more research conducted on the behavior and diets these fishes (Fig. 1). In addition, there may be instances in which cannibalism is reported for fish captured from natural habitats, when in fact these accounts represent cases of “net feeding” during the capture process (Fuentes and Quiroga 2012). Early life stages may be especially prone to net feeding, and opportunities for cannibalism greatly increases when small fish are captured and held, even momentarily, at abnormally high density within the confines of a net.

#### Prey developmental stages and predator–prey genetic relationship

Filial cannibalism was observed for 55 species, of which 25 involved fish in captive settings. Accounts involving wild fish are dominated by marine species of



**Fig. 1** Number of cannibalism reports for trophic guilds of the adult stage during seven decades (for most recent decade, data were only available from 2010 to 2015)

Gobiidae, Pomacentridae and Apogonidae that brood guard. For anchovies (Engraulidae) and other planktivorous species that ingest fish eggs, the genetic relationship of eggs is nearly impossible to confirm without DNA analysis. Consequently, reports of filial cannibalism usually have been based on direct observations of spawning and brood guarding fish in field (e.g., Okuda and Yanagisawa 1996; Payne et al. 2002) or laboratory settings (e.g., Petersen and Marchetti 1989; Payne et al. 2002).

Eggs are the development stage most frequently cannibalized, and this behavior is observed in diverse feeding guilds. Parents can consume either the entire clutch (total filial cannibalism) or only a few eggs (partial filial cannibalism), with the former viewed as an investment in future reproduction, whereas the latter influences both current and future reproductive success (Sargent 1992). Total filial cannibalism is expected when the cost of care is high, and may be influenced by brood size and age, parental body condition, local abundance of males, and degree of certainty of paternity (Kondoh and Okuda 2002; Manica 2004). Captive Egyptian mouth-brooders (*Pseudocrenilabrus multicolor*; Cichlidae) swallowed all remaining eggs from their clutch whenever their number fell below 20% of the initial number (Mrowka 1987). Nest guarding male *Telmatherina sarasinorum* (Telmatherinidae) cannibalized eggs when there was cuckoldry (Gray et al. 2007). When confronted with cuckoldry, nesting male bluegill sunfish (*Lepomis macrochirus*, Centrarchidae) adjusted parental care to favor broods more closely related to the male (Neff 2003). The presence of sneaker males during spawning can reduce certainty of paternity (Neff and Gross 2001; Neff and Sherman 2003); however, once the eggs hatch, the male can use chemical cues released by the fry to distinguish its offspring (Brown and Brown 1996; Neff and Sherman 2003, 2005). In addition, some eggs generally are not fertilized, and these are selectively consumed a few days after spawning (Mrowka 1987).

Filial egg cannibalism is usually restricted to males, possibly because males can gain significant additional energy, whereas females that consume their own eggs cannot regain all of the energy expended in gamete production (Kondoh and Okuda 2002; Manica 2002, 2004). Nevertheless, females have been observed cannibalizing other females’ eggs. Dark chub (*Nipponocypris temmincki*, Cyprinidae) females

are more cannibalistic than males, and females prefer to feed on the eggs of other individuals rather than their own (Katano and Maekawa 1996). Individual females have different propensities toward egg cannibalism, and cannibals and non-cannibals coexist within the same population, with cannibals having higher fecundity than non-cannibals (Katano and Maekawa 1996).

Parental nutritional status (body condition) has been shown to influence filial cannibalism (Kondoh and Okuda 2002; Manica 2002, 2004). Energetic costs associated with parental care, mainly in the form of egg fanning, together with reduced feeding opportunities may cause deterioration of the male's physical condition (Marconato et al. 1993). One potential response to reduced feeding opportunities during parental care is cannibalism of embryos (Rohwer 1978). Brood-guarding males, in particular, exhibit greater frequencies of cannibalism with declining body condition (Okuda and Yanagisawa 1996). Egg cannibalism could be a strategy primarily for obtaining energy as opposed to essential dietary nutrients (Svensson et al. 1998). The number of eggs eaten by male bullheads (*Cottus gobio*, Cottidae) was positively correlated with the number of egg masses in the nest (Marconato et al. 1993), possibly due to greater energy demand for care of larger broods. Egg cannibalism by males can also be influenced by female behavior. Garibaldi damselfish (*Hypsypops rubicundus*, Pomacentridae) males tend to cannibalize older eggs, apparently because females prefer to spawn with males guarding early-stage eggs rather than those guarding later stages. This runs counter to the assumption that older eggs possess higher reproductive value than younger eggs, and parents should therefore suffer a greater fitness deficit by consuming older eggs (Fitzgerald 1992; Sargent 1992).

For species with brood care, egg cannibalism can account for more than 90% of the energy required for reproduction (Pajaro et al. 1998), although some species cease feeding altogether while brood guarding (Coleman and Fischer 1991). Nonetheless, lack of foraging opportunities and low nutritional status are not prerequisites for filial cannibalism. In a laboratory experiment, male beaugregory (*Stegastes leucostictus*, Pomacentridae) receiving dietary supplementation grew faster but did not reduce cannibalism compared to males in control groups (Payne et al. 2002). Still, in some species lacking parental care, egg cannibalism

can account for more than 50% of the adult diet, particularly among certain zooplanktivorous species (Valdés et al. 1987; Brodeur and Merati 1993) and including cases in which males eat eggs even before completion of the spawning act (Nemtzov and Clark 1994). Razorfish (*Xyrichtys* spp., Labridae) were observed to eat ova both before and after fertilization (Nemtzov and Clark 1994). These authors hypothesized that males consumed eggs during unsuccessful spawning attempts, perhaps involving an ability to control sperm release so that they can trick females into releasing their eggs to provide the male with a food resource, a phenomenon termed intra-pair parasitism.

Cannibalism among larvae is strongly size dependent (Baras and Fortuné d'Almeida 2001), but exceptions are found in some species, including dorada (*B. moorei*) that have larvae that can consume conspecifics of equal size or even slightly larger than themselves (Baras et al. 2000b). Because larger eggs generally produce larger larvae, egg size heterogeneity promotes cannibalism (Rana 1985; Gisbert et al. 2000). Larger larvae from larger eggs that are able to cannibalize smaller larvae have accelerated growth, reduced vulnerability to predation (Folkvord 1991), and higher survival (Bagenal 1969; Rana 1985). Early hatching also may enhance survival during the larval stage if early hatched individuals can feed on smaller conspecifics (Pine et al. 2000).

As mentioned previously, cannibalism can occur within members of the same cohort (intra-cohort cannibalism) or between members of different cohorts (inter-cohort cannibalism), the latter including either the same or different year classes (Smith and Reay 1991). Inter-cohort cannibalism seems to be common (Smith and Reay 1991), with intra-cohort cannibalism less frequently reported and usually associated with crowded laboratory or aquaculture conditions (Sogard and Olla 1994). Intra-cohort cannibalism in the wild has been reported for a few species, including charrs, perch, pikes and walleye pollock (*Sander vitreus*, Percidae). Smith and Reay (1991) found no evidence of the occurrence of non-kin intra-cohort cannibalism of eggs. For this to occur, a species would need to have a prolonged spawning period so that fry hatched at the beginning of the spawning season could attain sufficient size to consume eggs spawned later in the season. Genetic analysis likely would be the only viable means to document non-kin intra-cohort cannibalism. A



requisite for inter-cohort cannibalism is co-occurrence of different age/size cohorts, which is influenced by a host of environmental and behavioral factors (Sogard and Olla 1993; Hjelm and Persson 2001; Adams and Wolfe 2006; Samhoury et al. 2009; Huss et al. 2010a; Borgström et al. 2015).

#### Factors affecting cannibalism

Many endogenous and exogenous factors affect fish cannibalism, and several studies have examined effects of food, light, and shelter availability in hopes of finding ways to reduce cannibalism in aquaculture facilities. Research has also been conducted on effects of medication on fish cannibalism. In one such study, males of the Siamese fighting fish (*Betta splendens*, Osphronemidae), a popular species in the ornamental fish trade, cannibalized their offspring even when dosed with Prozac (fluoxetine), a medication used to treat depression in humans (Forsatkar et al. 2014).

Aquaculture research has revealed that feeding frequency, food quantity and food quality influence cannibalism (e.g., Folkvord and Otterå 1993; Luz and Portella 2005; Tucker et al. 2006; Silva et al. 2014; Manley et al. 2015). As discussed previously, hunger and food scarcity are not requisite for cannibalism to occur (Payne et al. 2002), but can affect cannibalism rates. Rates of cannibalism often increase when alternative food resources are scarce, and rates may decline when alternative food resources are abundant. No evidence was found for cannibalism by pikeperch (*Sander lucioperca*, Percidae) in Lake Egirdir, Turkey, presumably this was due to the high abundance of big-scale sandmelt (*Atherina boyeri*, Atherinidae), an important prey of pikeperch (Yağcı et al. 2014).

Cannibalism is considered an asymmetric interaction, with larger animals generally consuming smaller ones (Polis 1981). Cannibalism was rare among *Arctic char* (*Salvelinus alpinus*, Salmonidae) smaller than 20 cm, but it increased with size among larger fish (Amundsen 1994). A similar observation was made for lesser sand-eels (*Ammodytes marinus*, Ammodytidae), with more cannibalism by larger individuals, including a specimen found with 18 small conspecifics in its stomach (Eigaard et al. 2014). Juvenile barramundi (*Lates calcarifer*, Latidae) selectively consumed the smallest size classes of conspecifics, despite being physically capable of ingesting larger individuals (Ribeiro and Qin 2015). This pattern was

hypothesized to be a function of higher cost associated with pursuit of larger prey that possess better escape tactics. Although large size disparity often induces cannibalism, certain species, such as piranhas (e.g., *Serrasalmus* spp. and *Pygocentrus* spp., Serrasalminidae) that remove pieces of flesh from their prey, are not limited by mouth gape and can feed on prey of similar or even larger sizes than themselves. Size disparity had little effect on rates of cannibalism in experiments conducted on the Amur catfish (*Silurus asotus*, Siluridae), a species that swallows prey whole (Yang et al. 2015).

In some species that have been tested, cannibalism appears to have a genetic basis. Hybrids between a cannibalistic poeciliid (*Poeciliopsis monacha*) and a non-cannibalistic species (*Poeciliopsis lucida*) revealed levels of cannibalism intermediate between those of the two parental species (Thibault 1974). Similar result was observed for hybrids of *Silurus meridionalis* and *S. asotus* that had rates of cannibalism intermediate between those of the pure species, but closer to those of the maternal parent (Yang et al. 2015). Cannibalism was population specific among *Arctic char* from four different regions, with populations from the Arctic region possessing stronger cannibalistic tendencies than *char* from more temperate regions (Amundsen et al. 1999). Similarly, populations of adult Northern pike (*Esox lucius*, Esocidae) from five lakes in northern Alberta fed on invertebrates rather than fish, and some populations fed on invertebrates almost exclusively (Beaudoin et al. 1999). In contrast, no genetic differences were observed between Atlantic cod (*Gadus morhua*, Gadidae) that were cannibals and those that were not, even though cannibals matured at larger sizes (Hardie and Hutchings 2011). In an experiment with *Arctic char* (*S. alpinus*), with consecutive lab trials followed by a release in natural lakes, cannibalistic tendencies of *Arctic char* depended on environmental conditions, densities of conspecific, alternative prey, and predator and prey size ratios, but genetic differences had no relationship (Svenning and Borgström 2005). In this experiment, *Arctic char* that never cannibalized in the experimental tanks turned to cannibalism when released in the lake, highlighting the potential difficulties in extrapolating laboratory results to natural settings (Svenning and Borgström 2005).

Cannibalism sometimes occurs when abundance of young-of-the-year conspecifics is high and alternative prey are scarce (Weyl and Hecht 1999; Grey et al.

2002; Dörner et al. 2007; Eigaard et al. 2014). For example pikeperch had high frequencies of cannibalism during years in which the density of age-0 conspecifics was high (Dörner et al. 2007). Cannibalism appears to be common among Cape hake (*Merluccius capensis*, Merlucciidae) when adults and juveniles are both abundant in the same areas (Macpherson and Gordoa 1994). Experiments revealed that adult European perch (*Perca fluviatilis*, Percidae) consumed more conspecifics than roach (*Rutilus rutilus*, Cyprinidae), because roach were better able to evade attacks (Christensen and Persson 1993). In lakes containing only perch and roach, juvenile perch cannibalized smaller conspecifics in years when roach hatched earlier than perch and were too large to be suitable prey (Heermann and Borcherd- ing 2013).

Environmental factors also can influence cannibalism. In freshwater habitats of Arctic regions, hypoxia and reduction of aquatic habitat due to freezing is stressful for most fishes. Certain fish species are resistant to these extreme environmental conditions, and some shallow habitats may be occupied by a single fish species, such as *Arctic char* (Berg et al. 2010), Northern pike (Beaudoin et al. 1999), or goldfish (*Carassius carassius*, Cyprinidae) (Tonn et al. 1994). High rates of cannibalism are a natural outcome under such circumstances. In a lab experiment, the placement of a light source in a safe zone that excluded adults reduced cannibalism of newborn guppies (*Poecilia reticulata*, Poeciliidae) that were attracted to light (Barki et al. 2014). Higher rates of cannibalism were observed during day than night, and newborn guppies avoided areas with adults during daytime. Similarly, sharp-tooth catfish (*Clarias gariepinus*, Clariidae) larvae showed more aggressive behavior in higher light intensities (Hossain et al. 1998; Mukai et al. 2013). In nature, cannibalism would be expected to be higher during periods when larvae and juveniles are more active. Because most marine fish larvae are visual feeders (Sierra-Flores et al. 2016), cannibalism should be higher during day than night. More cannibalism was observed in walleye pollock later in the day (1400–2100 hours) in sites where juveniles undergo extensive migrations in response to the presence of predators and/or absence of thermal stratification (Bailey 1989). Juveniles reduced migration when thermal stratification occurred, with young staying above and adults beneath the thermocline

(Sogard and Olla 1993). However, when all other factors are equal, cannibalism rate is expected to be a function of somatic growth rate of juveniles (Folkvord 1997).

In some cases, cannibalism appears more common in populations transplanted beyond the natural range of the species. For example, Amazonian tucunaré (or peacock cichlid, *Cichla* spp., Cichlidae) have been stocked in reservoirs throughout the tropics (Gomiero and de Braga 2004; Fugi et al. 2008; Gomiero et al. 2010) where they rapidly establish as a dominant species with cannibalism as high as 40% of the diet by frequency (dos Santos et al. 2001; Novaes et al. 2004; Fugi et al. 2008). Cannibalism was inferred to influence tucunaré population dynamics (Fugi et al. 2008) and slow the rate of invasion within the Upper Paraná Basin in Brazil (Kovalenko et al. 2010). South American silver croaker (*Plagioscion squamosissimus*, Sciaenidae), another Amazonian predator introduced into the Upper Paraná Basin, had higher rates of cannibalism during periods when conspecific density was high (Neves et al. 2015), suggesting that cannibalism could be a significant factor in population regulation. Extensive documentation of cannibalism in tucunaré populations in natural habitats (Jepsen et al. 1997; Winemiller et al. 1997; Winemiller 2001; Rabelo and Araújo-Lima 2002; Marto et al. 2015) counters Zaret's (1977) hypothesis that the peacock cichlid (*Cichla ocellaris*, Cichlidae) has evolved species-specific visual signals for avoidance of cannibalism.

#### Consequences of cannibalism

In his classic paper “*Stock and Recruitment*” (Ricker 1954), Ricker proposed that, within the restricted habitats of ponds and small lakes, cannibalism is one of the most likely methods of population regulation, especially for predatory species. He proposed that a larger adult stock not only increases the number of eggs laid and young produced in a given reproductive season, but it also reduces the survival rate of young. In some extreme situations, cannibalism may cause recruitment failure (Persson et al. 2000). Several empirical and experimental studies have supported Ricker's hypothesis, and inclusion of cannibalism sometimes can improve demographic models (Rudolf 2007) and stock management (Folkvord 1997). Harris (1975) stated that “Ricker's derivation is a difficult

one to fit in practice to marine species”, because most marine species are not strongly cannibalistic, in part due to spatial segregation between eggs and adults. Also, high levels of noise in population survey data and confounding effects of environmental variability make it difficult to demonstrate conclusively that cannibalism and other biotic interactions play significant roles in regulating fish stocks (Magnússon 1999a).

Cannibalism can act as a “life-boat mechanism” when food supply is insufficient to sustain a local population. When juveniles feed on a food resource that is inaccessible to adults, cannibalism of juveniles transfers this resource to adult biomass (Van Den Bosh et al. 1988). Predator–prey dynamics models showed that increasing cannibalism not only stabilizes systems and increases prey populations, but also can increase the predator population (Kohlmeier and Ebenhöf 1995). In contrast cannibalism can cause high juvenile mortality and low recruitment that leads to oscillations in population size (Magnússon 1999b).

When size differences within cohorts result in cannibalism (Rudolf 2006), cannibals grow faster than non-cannibals (Griffiths 1994; Berg et al. 2010; Huss et al. 2010b), which can result in bimodal size distributions. In a bimodal distribution, the smaller individuals generally feed on small aquatic invertebrates, and larger individuals are cannibals (Persson et al. 2003). Bimodal distributions favor cannibal growth and survival, the latter being strongly size dependent (Persson et al. 2000). Cannibalism is not the direct cause of bimodality (Griffiths 1994), rather it is the initial size variation after hatching and subsequent differences in individual growth rates that leads to bimodality (Byström et al. 2012). Formation of bimodal size distributions depends on several factors, including duration of the hatching period, cohort density and the food resource spectrum (Huss et al. 2010b). More research is needed to reveal the relative influence of these and other mechanisms causing multi-modal size distributions as well as the manner in which size distributions affect cannibalism in wild populations.

Cannibalism can promote transmission of diseases or parasites. Although diseased individuals often are more vulnerable to predation, the risk of contracting disease can be a selective force that reduces cannibalism (Pfennig et al. 1991, 1998). Unfortunately, there is scant information about how parasites and diseases are

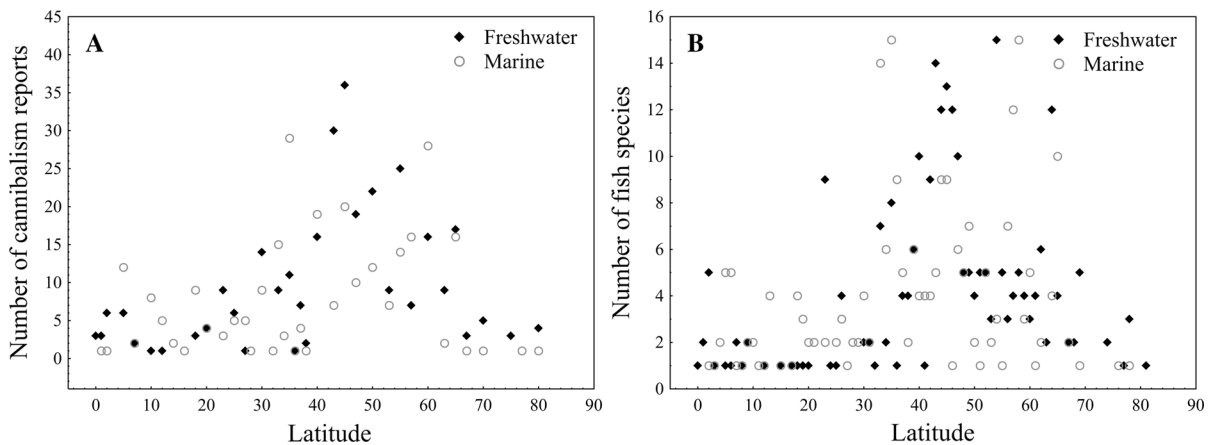
acquired by cannibalistic fish and their impacts on fitness and population dynamics. However, cannibalism is likely to be an ineffective mode of disease transmission in nature (Rudolf and Antonovics 2007). In aquaculture, fish not only consume conspecifics, but also may attack and damage them, which increases their susceptibility to bacterial and fungal infection (Gisbert et al. 2000).

#### A possible latitudinal gradient

Most reports of fish cannibalism in natural systems involve species from high latitude and alpine regions, such as *Arctic char*, Northern pike and Eurasian perch, that coexist with relatively few other fish species (Griffiths 1994; Persson et al. 2000; Berg et al. 2010; Borgström et al. 2015). Cannibalism might be less common in tropical freshwater and marine communities because: (i) on average, the probability of encounters with conspecific prey is much lower than encounters with heterospecific prey that collectively are much more abundant in species-rich, tropical communities (i.e., a functional response involving multiple prey taxa); (ii) many tropical species have co-evolved and therefore possess morphological and behavioral adaptations that reduce predation (Baras et al. 2010); (iii) most cannibalism is by piscivorous species, which have lower proportional abundance in tropical communities, or (iv) there is greater spatial segregation of adults and juveniles in the tropics (Harris 1975).

Cannibalism has been reported more often from high latitude than tropical regions (Fig. 2). Despite the fact that the data are regionally biased (more publications from North America and Europe), cannibalism seems to be more common at from higher latitudes. Griffiths (1994) reported that cannibalism by *Arctic char* increases with latitude. *Arctic char* are found throughout arctic, subarctic, boreal and temperate regions of the Holarctic (Klemetsen et al. 2003), and this species provides an excellent model to test the latitudinal hypothesis. Because frequency of cannibalism is partially a function of the rate of encounter between individuals of the same species (Fox 1975b), cannibalism might be lower in the tropics because of high species diversity (Stuart-Smith et al. 2013). Most fish cannibalism involves invertivorous species and predation on early life stages; therefore, even if communities at higher latitudes have greater piscivore





**Fig. 2** Number of cannibalism reports (a), number of species for which cannibalism was reported (b) in relation to latitude for freshwater (black) and marine (grey) habitats

abundance or higher proportions of piscivorous fish species (Moss 2013), it should not greatly influence the frequency of cannibalism. Greater species diversity and evenness found in the tropics should reduce the frequency of cannibalism if alternative prey taxa are encountered more or less in proportion to their relative abundances. If indeed cannibalism is more common at higher latitudes where fish diversity is lower, it could have a significant influence on population dynamics as discussed above.

Why are some species more cannibalistic than others?

This is a question that needs further research, but some general hypotheses can be proposed. Cannibalism frequency varies among species, e.g., from 15% in Arctic cod to 65% in walleye pollock (Juanes 2003). In the case of *Arctic char*, cannibalism may be a behavior learned during the larval stage. Larval char are zooplanktivores, and when zooplankton is scarce, smaller conspecifics provide a viable dietary alternative. Cannibalistic juveniles have a nutritional advantage and grow faster than non-cannibals within their cohort, which reinforces bimodality of the size distribution. Cannibalism may be more common than interspecific predation within certain populations, with many adults preferentially exploiting conspecifics rather than heterospecific prey (Byström et al. 2013). Most evidence of preferential consumption of conspecifics comes from experimental studies, which should be interpreted with caution. For

example, nine-spine sticklebacks (*Pungitius pungitius*, Gasterosteidae) were used as the interspecific prey in experimental study of cannibalism by *Arctic char* (Byström et al. 2013). Sticklebacks are well defended by spines and plates (Reist 1980; Christensen and Persson 1993), whereas young char have soft bodies and fins that are relatively easy to handle during capture and ingestion. More tests are needed to evaluate this preference for cannibalism hypothesis.

Many fish species have not yet revealed evidence of cannibalism in nature, even though they are cannibalistic in aquaculture settings. Some of these species (e.g., *Brycon*, *Salminus*, *Colossoma* and *Pseudoplatystoma* spp.) are tropical freshwater fishes that undergo seasonal migrations for spawning, and therefore adults usually are found in locations and habitats different from those occupied by their early life stages (Wine-miller and Jepsen 1998). This migratory behavior creates spatial segregation between young and adults. Some freshwater species have eggs and larvae that drift great distance in river currents, which should cause in spatial segregation not just between adults and juveniles, but also between different juvenile cohorts.

Another factor, perhaps the most important one, influencing cannibalism is mouth gape in relation to prey size. Gape limitation differs among species and ontogenetic stages owing to allometric growth of mouth and body dimensions. Piscivores and other macrophagous predators tend to have large mouth gapes with less ontogenetic allometry compared to most other feeding guilds (Scharf et al. 2000; Baras

and Jobling 2002). Consequently, these fishes can become cannibalistic during early developmental stages and can continue to feed on smaller conspecifics throughout their lives. Nonetheless, gape allometry varies widely among diverse predatory fishes, and gape limitation is not the only size-based factor to influence feeding strategies. Predator foraging tactics, specialized morphology (e.g., oral jaws, teeth, gill rakers, pharyngeal apparatus), migratory behavior as well as prey defensive behavior (crypsis, speed, maneuverability, aggression) and morphology (body depth, spines, armor) also influence predator–prey interactions (Scharf et al. 2000; Inoue et al. 2016).

#### Future directions

Given the growing emphasis on aquaculture to increase food supply, research is clearly needed to reduce cannibalism among fish held at high densities in captivity. At the same time, the commonness of cannibalism and its causes and consequences for fishes in nature remain poorly understood. Cannibalism has been described as being widespread in fish (Smith and Reay 1991), and yet it has been reported for only about 1% of the approximately 30,000 marine and freshwater teleost fishes worldwide (Lévêque et al. 2008), with most accounts from aquaculture settings. One might then ask—why are there so few reports of fish cannibalism? Eigaard et al. (2014) found the lack of field observations of fish cannibalism surprising, given the fact that most fishes have external fertilization, pelagic larvae and reproductive strategies that favor offspring quantity rather than offspring size.

Perhaps cannibalism actually is rare among wild fishes, and occurs only when there are occasional opportunities. Most fish may rarely encounter small conspecifics or are incapable of pursuing, capturing and ingesting them. Or perhaps cannibalism is more common than indicated by currently available evidence. Dietary studies may fail to document cannibalism due to inadequate methodologies or lack of interest to search for it. Perhaps most species have evolved effective mechanisms to avoid cannibalism because it reduces inclusive fitness. On the other hand, there is new evidence that cannibalistic behavior has a genetic component, which suggests a potential fitness advantage.

The role of cannibalism in population dynamics is still controversial. Some have proposed that

cannibalism is a critical mechanism of density-dependent regulation, but others have concluded that cannibalism has little or no importance for population dynamics. Many research opportunities exist for addressing how cannibalism is influenced by population size distributions, ontogenetic variation in morphology and behavior, local community structure, habitat heterogeneity, and abiotic environmental factors. In addition to ecological modeling, comparative field studies and controlled lab and field experiments are needed to address these questions.

Our review found evidence of cannibalism in hundreds of fish species, including many accounts from wild populations, but this represents a tiny fraction of global fish species richness. Much more effort is required to overcome the many potential sources of bias in the current body of evidence. For example, eggs and larvae, the stages most vulnerable to predation by conspecifics, are difficult to identify visually to species level during stomach contents analysis, and are digested even more rapidly than small fish. Development of new techniques, such as molecular methods, would greatly improve estimates of predation on early life stages. Better documentation and understanding of fish cannibalism would contribute not only to improved aquaculture, but also to management of wild fish stocks, conservation of threatened species, and mitigation of impacts from invasive species.

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