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MYXOZOA

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Phylum Cnidaria

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doi: 10.32873/unl.dc.ciap013

2024. In S. L. Gardner and S. A. Gardner, eds. Concepts in Animal Parasitology. Zea Books, Lincoln, Nebraska, United States.

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Chapter 13

Myxozoa (Subphylum)

Terrence L. Miller

Aquatic Diagnostics Laboratory, Department of Primary Industries and Regional Development–Western Australia, Perth, Western Australia, Australia; and School of Veterinary and Life Sciences, Murdoch University, Perth, Western Australia, Australia
terry.miller@dpird.wa.gov.au

Reviewer: Christopher M. Whipps, Center for Applied Microbiology, College of Environmental Science and Forestry, State University of New York, Syracuse, New York, United States

Introduction

Images that often come to mind upon hearing or seeing the word Cnidaria are swarms of jellyfish following the sun around lakes in Palau or the colorful tropical coral reef ecosystems with their vast diversity of hard and soft corals, and anemones housing charismatic clownfish. Rarely do images of parasites come to mind. However, recent phylogenetic and protein expression analyses have revealed the diverse group of obligate endoparasites of the subphylum Myxozoa (Grassé, 1970) (once considered a phylum in its own right) are in fact morphologically simplified, although highly specialized, cnidarians (Atkinson et al., 2018; Collins, 2009; Shpirer et al., 2018; Zrzavy and Hypsa, 2003). The primary uniting morphological feature of this group is the presence of a nematocyst-like structure termed the polar capsule in the myxozoan descriptive literature, which contains the polar filament that fires off in the presence of a suitable host, similar to the firing of nematocysts in free-living cnidarians used to capture prey (Figure 1).

The Cnidaria contained only 10 parasitic species previously, all of which had free-living stages at some point in their life cycle. The impacts of this seemingly innocuous change in classification now result in the once relatively parasite-free Cnidaria, now consisting of approximately 20% obligate parasites of a wide range of vertebrate and invertebrate hosts (Atkinson et al., 2018). This newly recognized and unique adaptive diversification of endoparasitic Cnidaria reveals that they are incredibly diverse in their specializations and ecologies, and greatly affect aquatic animal health in wild and cultured animal production systems.

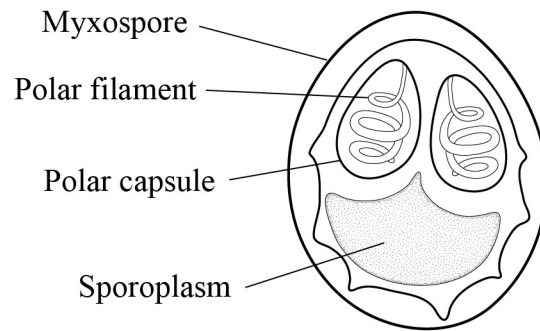


Figure 1. An uncharacterized species of *Myxobolus* (subphylum Myxozoa: class Myxosporea) found in *Acanthopagrus australis* from Moreton Bay, Australia illustrating the coiled nematocyst-like polar filament structure and general morphological characters. Source: T. Miller. License: CC BY-NC-SA 4.0.

Classification and Host Associations

The subphylum Myxozoa currently contains over 2,400 species in 2 disparately populated classes, the Malacosporea Canning et al., 2000, which currently consists of 2 genera (*Buddenbrockia* Schröder, 1910 and *Tetracapsuloides* Canning et al., 2002), and the Myxosporea Bütschli, 1881, which has over 60 genera (Atkinson et al., 2018). Generally, species within both classes require 2 hosts (an invertebrate as the definitive host and a vertebrate as the intermediate host) to complete their life cycle. The primary biological characteristics that distinguish the 2 groups are that malacosporeans use freshwater bryozoans and myxosporeans use marine or freshwater annelids as their invertebrate hosts (Patra et al., 2017). Species of both classes predominantly infect fish as their vertebrate host (> 95% of all reported species), however, a number of myxosporean taxa have now been reported from mammals, waterfowl, amphibians, and reptiles (Bartholomew et al., 2008; Hallett et al., 2015).

The fluid nature of taxonomic classification, especially above the level of the family, is demonstrated with respect to the Myxozoa due to the many hypotheses regarding the origin of these species and the nature of the evidence used to classify the group over the last couple of centuries. Their microscopic size and simple spore morphology led to the initial classification of myxozoans that were discovered in the early to mid-1800s as belonging to the Sporozoa, a group of unicellular spore-forming organisms in early literature (Okamura and Gruhl, 2015). Multicellularity of these organisms was identified in the late 19th century, but it wasn't until 1970 that the Myxozoa was formally considered a phylum in the Metazoa (Grassé, 1970; Štolc, 1899). Subsequent DNA sequence analyses of the nuclear small subunit ribosomal DNA

region (SSU rDNA) of myxozoans revealed their close phylogenetic relationships with the Cnidaria (Kent et al., 2001; Siddall et al., 1995).

Prior to 1994, classifications of the Myxozoa (that is, when it was then considered a phylum) contained 2 subclasses, the Myxosporea and Actinosporea, which were characterized based on distinctly different spore morphology and host associations (fish and annelids, respectively). It wasn't until experimental work investigating the transmission of *Myxobolus cerebralis* (the causative agent of whirling disease in salmonids) revealed that the markedly dissimilar spore morphologies observed in the annelid and fish hosts were actually just different developmental spore stages of the same organism (Markiw and Wolf, 1983; Wolf et al., 1986). Actinosporea was subsequently suppressed as a taxon (Kent et al., 2001; Kent and Margolis, 1994). Currently, DNA markers are primarily used (experimental infection trials less commonly) to determine conspecificity of actinospore and myxospore stages recovered from infected intermediate or definitive hosts (Hallett et al., 2002).

Life Cycle Stages and Infection Dynamics

Reproduction within the Myxozoa is as diverse as that observed within the free-living Cnidaria. Asexual and sexual reproduction in the Myxozoa are complex and detailed aspects of haploid and diploid cell formation within the group remains unknown. Evidence to date suggests meiosis generally occurs in the annelid or bryozoan host, which indicates these are the definitive hosts for these taxa (Okamura et al., 2015b). Transmission of myxosporean infections occurs through the production and release of actinospores from the annelid host and myxospores from the vertebrate host (Eszterbauer et al., 2015). Malacosporean transmission is similar in that infectious malacospores are released by the bryozoan host and the spores released from the fish host are characterized as fish malacospores (Hartikainen and Okamura, 2015; Patra et al., 2017).

Research into the causative agent of proliferative kidney disease (PKD), a significant disease impacting wild and cultured salmonids infected with *Tetracapsuloides bryosalmonae*, resulted in the original implication of bryozoans as hosts involved in the life cycle of this malacosporean pathogen (Hartikainen and Okamura, 2015). This and subsequent research into species of *Buddenbrockia*, which infects cypriniform and perciform fish, has contributed to the bulk of knowledge on the transmission and developmental stages of malacosporeans in their bryozoan and fish hosts (Hartikainen and Okamura, 2015; Patra et al., 2017). Malacospores in fish develop and mature in the kidney tubules and are released into the environment through urine excretion and infect the

bryozoan host through ingestion of infectious spores or direct contact (Patra et al., 2017). Development within the bryozoan host results in the formation of multiple sac- or vermiform-like (termed myxoworm) stages containing many spores. These stages then burst inside of the bryozoan and spores are released into the water column via the vestibular pore (Hartikainen and Okamura, 2015; McGurk et al., 2006; Patra et al., 2017). Fish become infected when malacospores contact the gills or epidermis, the nematocyst-like polar filament everts to facilitate attachment, and the amoeboid sporoplasm invades the adjacent tissue (Hartikainen and Okamura, 2015).

Waterborne stages of individual myxosporean species released from the invertebrate and vertebrate hosts are often so morphologically dissimilar in appearance that, as discussed above, their original taxonomic classifications were unclear. The annelid hosts of myxosporeans vary depending on their occurrence in marine or freshwater environments. In freshwater ecosystems worldwide, oligochaetes are much more species rich than polychaetes ($\approx 1,000$ versus ≈ 170 species, respectively); whereas in marine ecosystems, oligochaetes are vastly outnumbered in species diversity by polychaetes (≈ 200 versus $\approx 12,000$ species, respectively). Consequently, and possibly as a byproduct of coevolutionary radiation, the known annelid hosts of myxosporeans are primarily oligochaetes in freshwater and polychaetes in marine ecosystems (Alexander et al., 2015), although it should be noted that the life cycles are known for only very few species overall.

Infection of the annelid host is initiated via contact with infectious myxospores released from the vertebrate host (predominately fish). The site of infection in the fish host plays an important role in how myxospores are released into the environment. For example, species that form cyst-like pseudoplasmodia containing many infectious myxospores in various fish tissues (for example, in skeletal muscle, organs, or viscera), generally rely on the death of the host and post-mortem changes (decomposition or digestion) to facilitate spore release. For taxa present in marine ecosystems, direct predation or scavenging of fish harboring tissue-dwelling myxosporeans may be an important mode of viable spore release and spread in the environment through fecal material which settles in the benthos for exposure to their suitable annelid host. Species which develop mature spores in the biliary or urinary tracts of their fish hosts (for example, *Ceratomyxa* spp. or *Myxidium* spp.) are released directly into the environment through excretion of feces and urine.

Infection of the annelid host is considered to be primarily via ingestion of myxospores, although infection by direct contact with spores and amoeboid sporoplasms invading through the epidermis is likely (Alexander et al., 2015).

Once within the annelid host, the parasite then migrates to the preferred site of infection (for example, intestinal epithelium or body wall) and proceeds to undergo proliferative phases including schizogony, sporogony, and gamogony to produce numerous actinospores (Alexander et al., 2015; Eszterbauer et al., 2015; Hallett et al., 1999). Actinospores are then released into the water through the anus or epithelium of the annelid host by mechanisms which are still unclear (Alexander et al., 2015). Actinospore stages often have large caudal processes that presumably facilitate buoyancy and dispersal within the water column in order to come into contact with their suitable fish host. Infection of the fish host is through, 1) the anchoring of the actinospore to the gills or epithelium via the discharged polar filaments, and 2) the spore valves releasing the infectious sporoplasm, which 3) invades the adjacent epidermis and 4) subsequently migrates to the preferred site of infection (Kallert et al., 2015).

Diagnosics and Characterization

Diagnostic identification and taxonomic characterization of myxozoans via morphology only are complicated by the relatively few distinct morphological characters that can be used to discriminate between taxa. Most formal species descriptions of malacosporeans and myxosporeans are of the stages present in their vertebrate hosts, with taxa causing disease receiving particular attention. Descriptions of taxa generally incorporate characters such as **spore** size, shape, **pseudoplasmodia** dimensions and numbers of **spore valves**, **polar capsules** (including location and orientation), and coils of the **polar filaments** contained within being particularly important (Lom and Dyková, 2006; Patra et al., 2017). Other biological or ecological characteristics that are often important information accompanying species descriptions and aiding discrimination between taxa are the host species infected, tissue tropism, or site of infection. One of the most useful reviews and pictorial overviews for identification of myxozoan genera for someone new to the field is that of Lom and Dyková (2006; see Figure 2).

Currently, the inclusion of DNA sequence data as accompanying characters used to discriminate taxa are becoming critical for revealing taxonomic, ecological, and evolutionary relationships that were previously unresolved. The most common genetic markers used for comparative phylogenetic analyses and species-level distinction are the nuclear large and small subunit ribosomal DNA regions (LSU rDNA and SSU rDNA), which account for the majority of genetic data available on the publicly accessible databases GenBank and EMBL (Atkinson et al., 2015; Fiala, 2006). These ribosomal sequences contain a combination of highly conserved and variable regions, which correspond to the stem and loop

motifs of the folded ribosome involved in the protein production machinery of eukaryotic cells. This combination allows for the robust alignment of conserved regions for phylogenetic or primer design purposes, and enough variability to reliably distinguish different sequence variants (Atkinson et al., 2015).

The consensus to date is that new species descriptions or revisions of taxonomic affinities within the Myxozoa should attempt to incorporate a combination of morphological characters (that is, examined via traditional microscopic and ultrastructural techniques), tissue tropism, host associations (including life cycle and host specificity data if possible), and DNA sequence data (Atkinson et al., 2015). The usefulness of these robust taxonomic treatments has been demonstrated through recent advances in knowledge of the biodiversity and ecology of myxozoans in aquatic ecosystems. Extraordinary species richness of myxozoans in aquatic environments is being revealed through recent biodiversity surveys, with some estimates suggesting the species diversity of myxozoans exceeds that of the number of fishes present in these ecosystems (Gunter and Adlard, 2008; 2009; Heiniger et al., 2011).

Aquatic Animal Health Implications

Much understanding of the biology, life cycles, and transmission dynamics of myxozoans has been prompted by investigations into the severe pathology and disease elicited by some myxozoan taxa, which cause significant negative economic and population-level impacts in aquatic wildlife and aquaculture. A few of the major diseases or production issues due to myxozoan infections are mentioned here to illustrate these impacts.

Proliferative Kidney Disease Caused by the Malacosporean *Tetracapsuloides bryosalmonae*

Proliferative kidney disease (PKD) is a condition which results in significantly high mortality rates in salmonid fish in Europe and North America caused by infections with the malacosporean *Tetracapsuloides bryosalmonae* (Canning et al., 1999). This disease is characterized by marked immunosuppression of the host, the proliferation of the parasite in kidney interstitia resulting in chronic hyperplasia and granulomatous reactions that cause distinct splenomegaly, renomegaly, and pathology in affected renal tissues (Sitjà-Bobadilla et al., 2015). Freshwater bryozoans of the class Phylactolaelmata have been identified as hosts of this species. Infections in both the bryozoan and fish hosts appear to be temperature dependent, with higher prevalence and intensities observed in warmer months (Jones et al., 2015). The combination of habitat loss and degradation, warming climate, and impacts of PKD have been implicated in the decline of vulnerable trout populations throughout their native ranges.

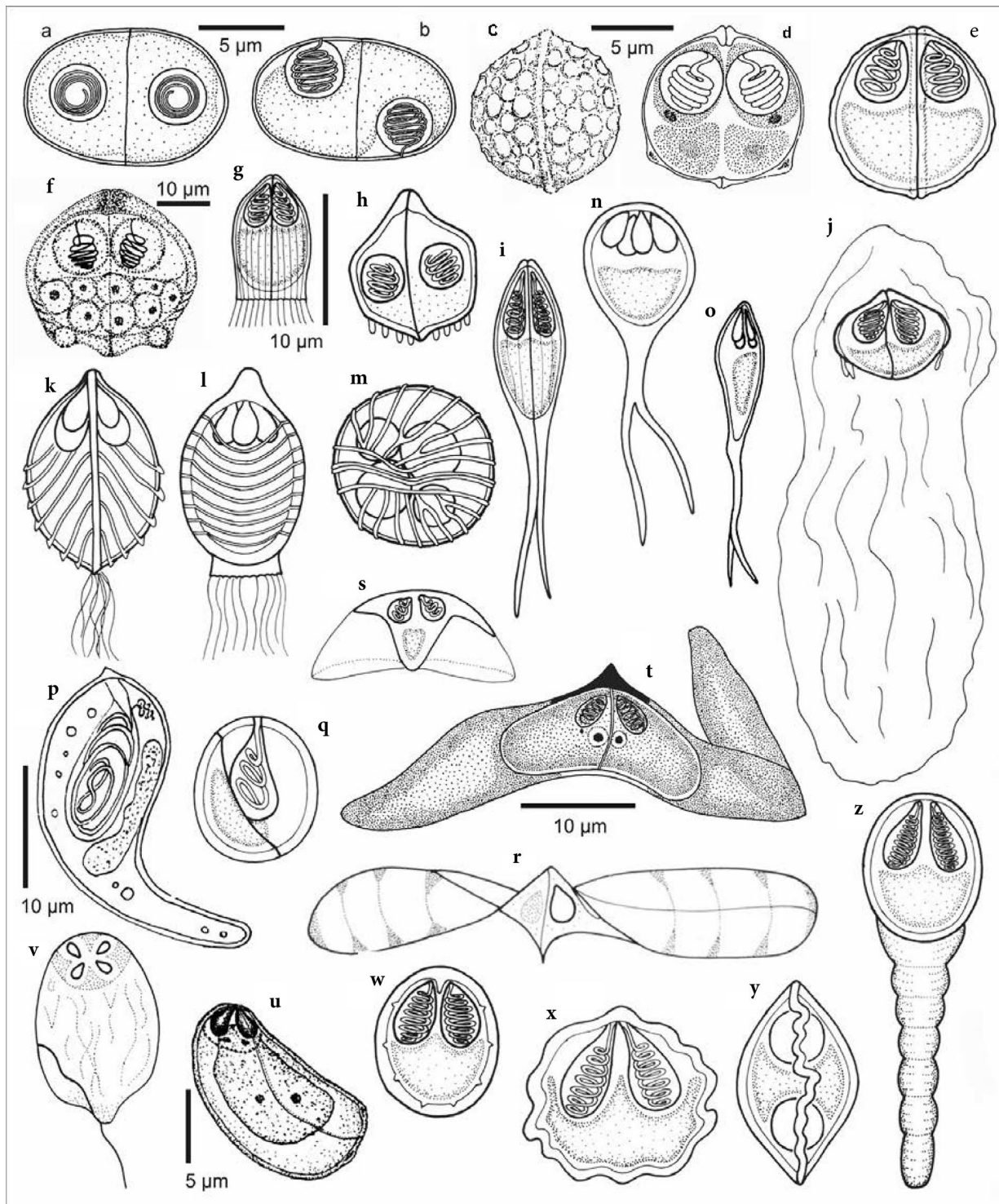


Figure 2. Line drawings of myxosporean spores. *Ellipsomyxa gobii* in (a) apical and (b) sutural view (adapted from Kōie, 2003). *Sphaerospora elegans*, (c) pitted spore surface, (d) sutural view (Feist et al., 1991). *e) Sphaerospora renicola* in sutural view. *f) Polysporoplasma spariss* in sutural view (adapted from Sitjà-Bobadilla and Alvarez-Pellitero, 1995). *g) Hoferellus cyprini* in sutural view. *h) Wardia ovinocua*. *i) Myxobilatus gasterostei* in sutural view. *j) Palliatus mirabilis* in sutural view. *Chloromyxum leydigi* in (k) sutural and (l) frontal view. *m) Chloromyxum cristatum* in apical view. *n) Caudomyxum nanum*. *o) Agarella gracilis*. *p) Auerbachia anomala* (adapted from Meglitsch, 1968). *q) Globospora sphaerica*. *r) Alatospora samaroides*. *s) Pseudoalatospora scombri*. *t) Renispora simae* (adapted from Kalavati, 1996). *u) Parvicapsula asymmetrica* (adapted from Shulman and Shulman-Albova 1953). *v) Neoparvicapsula ovalis*. *w) Myxobolus muelleri*. *Spirosuturia carassii* in (x) frontal and (y) apical view. *z) Unicauda clavicauda*. Sources: Lom and Dyková (2006) and adapted from sources noted in-line. License for all: CC BY.

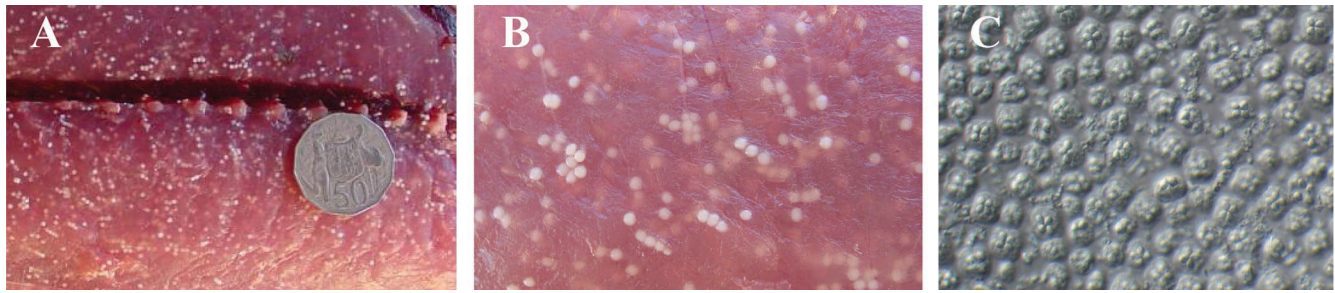


Figure 3. *Kudoa* sp. pseudoplasmodia in the flesh of a tuna collected off Ningaloo Reef, Western Australia. A) Macroscopic view with an Australian 50-cent piece for size reference B) Close up of macroscopic pseudoplasmodia in flesh, and C) Photomicrograph of spores released from pseudoplasmodia showing the 4 valves and 4 polar capsules characteristic of this this group. Source: T. Miller. License: CC BY-NC-SA 4.0.

Whirling Disease

Infections with the myxosporean *Myxobolus cerebralis* can cause the condition called whirling disease in salmoniform fish. As its name suggests, clinical signs of disease are characterized by the distinct erratic whirling patterns swum by affected individuals and a distinct darkening of the caudal region (Jones et al., 2015). *Myxobolus cerebralis* is one of the few known chondrophilic, or cartilage preferring, species. Development of the pseudoplasmodia primarily occurs in the cartilage of the head and vertebrae, and compression of the brain and medulla spinalis results in the abnormal swimming behavior observed in infected fish (Molnár and Eszterbauer, 2015). Discovery of the annelid host, *Tubifex tubifex*, as the obligate invertebrate host required to complete the life cycle, led to a revolution in understanding of myxosporean development and transmission (Jones et al., 2015).

Whirling disease has resulted in substantial decreases in susceptible salmonid populations throughout its known range, which is now considered distributed almost circumglobally wherever *Tubifex tubifex* is found. A notable exception is Australia, which is currently considered free of *Myxobolus cerebralis*. There it remains on the list of nationally notifiable diseases and strict quarantine measures are in force to reduce the possibility of incursion of this parasite, which could have devastating impacts to naïve salmonid populations on the relatively isolated island continent.

Myxosporean Infections and Seafood Marketability

In contrast to the myxozoan infections briefly mentioned in the above sections, some myxosporean species do not cause significant health issues or severe pathology in their host fish, but negatively impact the production and trade of seafood post-harvest. This is primarily due to the presence of unsightly macroscopic cyst-like pseudoplasmodia in flesh or myoliquefaction of infected musculature, external

surfaces, or viscera. For example, a number of species of *Kudoa* are known to produce distinctly white, macroscopic pseudoplasmodia in muscle tissue of tuna species that stand out dramatically against the pink/crimson flesh of fresh fillets and render them effectively unmarketable for human consumption (Figure 3) (Moran et al., 1999). Another major marketability issue encountered in fish harvested from the wild or produced in aquaculture is post-mortem myoliquefaction, which results in mushy or butter-like consistency of fish muscle when cooked (Kristmundsson and Freeman, 2014; Langdon, 1991; Langdon et al., 1992; Moran et al., 1999). This is due to the presence of myxosporean pseudoplasmodia (often *Kudoa* or *Unicapsula* spp.) residing in myofibrils of infected fish releasing a suite of protease or proteolytic enzymes once the host has died, presumably an evolutionary adaptation to facilitate rapid release from the host into the environment (Alama-Bermejo et al., 2009; Lester, 1982; Stephens and Savage, 2010). Enzymatic breakdown of muscle tissue via this protease activity is accelerated in the presence of heat, not a particularly desirable combination when the product being marketed is destined for cooking prior to human consumption. High intensity infections can result in fish fillets subjected to heat via cooking displaying the consistency of jelly or peanut butter, which can elicit complaints from patrons visiting a restaurant or guests around the family barbecue.

Myxozoan infections and associated disease or marketability issues have had major negative impacts on wild fisheries and the aquaculture industries worldwide (Jones et al., 2015; Kent et al., 2001; Okamura et al., 2015a). Despite the significant progress made over the last few decades in the understanding of myxozoan biology, much remains unknown. From a biodiversity perspective, while around 2,400 species have been described, it appears that the surface has barely been scratched to discover the total myxozoan species richness of the world's freshwater and marine

ecosystems. In addition, less than 1% of all myxozoan species have had their complete life cycles elucidated and all susceptible hosts for particular species resolved. Further investigations into the diversity, host specificity, ecology, and transmission dynamics are clearly required to help mitigate the impacts of known and emerging diseases associated with myxozoan infections.

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