

MULTIVALVULID MYXOZOA IN FISH

Kudoa, *Unicapsula*

(animal: myxozoan)

Overview

Myxozoans are obligate parasites which produce unique multicellular spores comprised of valvogenic, sporoplasmic and capsulogenic cells. The latter form polar capsules with extrudible filaments (similar to cnidarian nematocysts — but used for attachment). They were originally classified as protistan organisms, but ultrastructural and molecular studies have indicated that they are bilateral metazoans, and are now classified as animals (cnidarians). Many species have been described as coelozoic or histozoic parasites in fish and some in amphibia, reptiles and various invertebrates (especially oligochaetes, polychaetes and sipunculids). Parasite development is characterized by vegetative proliferation of trophozoites (by formation of multinucleate plasmodia containing generative cells) followed by spore morphogenesis (by formation of pansporoblast through union of pericyte and sporogonic cells and differentiation of the latter to form valvogenic, capsulogenic and sporoplasmic cells which produce the spore valves, nematocyst-like polar capsules and amoeboid infective sporoplasms). The life-cycles of several myxozoan species have been found to involve cyclic development between myxospore stages in fishes and actinospore stages in worms. Two major myxosporean orders are recognized: the Bivalvulida (spores with two shell valves) and the Multivalvulida (spores with more than two shell valves). Numerous multivalvulid species occur as histozoic or coelozoic parasites of freshwater and marine fish. Kudoid species form stellate spores, most with 4 valves and 4 polar capsules, and infections have been associated with tissue cysts and myoliquefaction, particularly in the muscles of tuna.

Classification:

Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Phylum: Cnidaria (diploblastic, radial symmetry, cnidocytes with nematocysts, sea anemones, corals, jellyfish, hydrozoa, myxozoa)
Subphylum: Myxozoa (form multicellular valved spores with polar filaments)
Class: Myxosporidia (spores with 1-2 sporoplasms, 1-13 polar capsules)
Order: Multivalvulida (radially symmetrical spores, 2-13 valves, polar capsules grouped together at apex)
Family: Kudoidae (4-13 valves and polar capsules (rarely 2), mainly histozoic in muscles of marine fish)
Genus: *Kudoa* (histozoic parasites in fish)
Species: various species cause lesions in fish muscles
Family: Trilosporidae (three valves and polar capsules, coelozoic/histozoic in marine fish)
Genus: *Unicapsula* (parasitic in muscles of fish)
Species: various species cause lesions in fish

Parasite biodiversity and host range: Myxozoans are unique parasites that form multicellular (pluricellular) spores (with valves, polar capsules and infective sporoplasms) in cold-blooded vertebrates and worm-like invertebrates. Despite their multicellularity, they were often classified together with the unicellular spore-forming protozoa (Protista), more for convenience than for phylogenetic relationships. Contemporary ultrastructural and molecular studies have now shown that they are bilateral metazoan animals, and are now classified with the Cnidaria (jellyfish and allies). Myxozoa polar capsules contain extrudible filaments similar in structure to cnidarian nematocysts, but they are used for attachment to host cells during the infection process (rather than for stinging). Numerous myxozoan species have been described as coelozoic or histozoic parasites predominantly in fish (marine and freshwater) throughout the world, as well as in some amphibia, reptiles, annelids (oligochaetes and polychaetes) and sipunculids. Some 3,110 species have been described but little is known about their host specificity. Conventional taxonomic classification schemes recognized two major myxozoan assemblages which were quite different in morphology and biology: the classical Myxosporidia in fish, and the enigmatic Actinosporidia in annelids. Little was known about their complete life-cycles and modes of transmission, until recent studies demonstrated that several species had heteroxenous (2-host) life-cycles alternating between myxospores in fish (acting as intermediate hosts) and actinospores in annelids (acting as definitive hosts). This prompted most taxonomists to suppress actinosporidian nomenclature pending recognition of complete life-cycles. The anchor-shaped actinospores found in annelids have subsequently been assigned to 19 collective groups with vernacular names (anton-, auranti-, echin-, hex-, hung-, ormier-, pseudtri-, seis-, sphaer-, syn-, tetra-, tri-, unicapsul-actinomyxon, neoactinomyxon, endocapsa, guyenotia, raabeia, siedleckiella, and tetraspora), whose affinities to myxosporean stages have yet to be determined. Contemporary classification schemes now recognize 2 myxozoan classes: the Malacosporidia containing species with soft shell valves and enigmatic worm- and sac-like trophic stages; and the Myxosporidia containing species with hardened shell valves enclosing sporoplasmic and capsulogenic

cells. Two major myxosporean orders are recognized: the Bivalvulida (spores with 2 shell valves) and the Multivalvulida (spores with more than 2 shell valves).

No. families	No. genera	No. species	Hosts	Location
Class: MALACOSPOREA (spores with soft (unhardened) shell valves)				
Order: Malacovalvulida (worm-like (myxoworm) and sac-like trophic stages)				
1	2	3	bryozoa, salmonid fish	histozoic, coelozoic
Class: MYXOSPOREA (myxospores with hardened shell valves enclosing sporoplasmic and capsulogenic cells)				
Order: Bivalvulida (spores with two valves)				
Suborder: Platysporina (polar capsules at one pole in sutural plane)				
1	13	1,622	fish (mostly freshwater)	histozoic
Suborder: Variisporina [Eurysporina (Unipolariina) + Bipolarina] (polar capsules perpendicular to sutural plane)				
15	48	1,323	fish (mostly marine), some amphibians	mostly coelozoic, some histozoic
Order: Multivalvulida (radially symmetrical spores, 3-13 valves (rarely 2), polar capsules grouped together at apex)				
3	5	163	fish (marine)	mostly histozoic, some coelozoic

Collectively, around 3,110 species of myxozoan parasites have been described in over 2,000 species of fish (belonging to 332 families in 89 orders) as well as in some amphibians, a few reptiles, and rarely in shrews, birds and even as hyperparasites in some trematodes. Myxospores have been recorded in over 800 species of marine fish (from 233 families in 64 orders) and over 1,120 species of freshwater fish (from 124 families in 35 orders). Myxozoan classification still depends largely on myxospore structure (principally shape, number and position of shell valves and polar capsules), and sometimes on their presumed specificity (host occurrence and tissue tropism). With improvements in microscopic techniques, there have been many reports and reviews of myxozoan taxa over the last century. With the recent advent and utilization of molecular characterization techniques, new light has been cast on phylogenetic relationships, which sometimes do not agree with morphotypic and biologic classifications. Many myxozoan groups have been found to be polyphyletic, with broader host specificities than previously thought and many clades aligned with host habitats. For example, molecular studies on members of the bivalvulid genus *Leptotheca* showed them not to be monophyletic, but to align variously with the genera *Ceratomyxa*, *Ellipsomyxa*, *Sphaerospora*, and *Myxobolus*, to which they were subsequently re-assigned. Genotypic characterization of multivalvulid species with 5-13 valves and polar capsules (originally placed in the diverse genera *Pentacapsula*, *Hexacapsula* and *Septemcapsula*) have grouped together with the genus *Kudoa* (typically with 4 polar capsules), to which they have all been re-assigned. The identity of many more species (and genera) have been reappraised following comparative molecular studies, so the contemporary literature has become riddled with numerous revisions resulting in many synonyms. All attempts have been made in the following tables to record such nomenclatural changes. Three multivalvulid families have been recognized, collectively containing around 150 species allocated to 5 genera. Most species are found as histozoic and some coelozoic parasites, mainly in marine fish. Several species have been associated with clinical diseases in their hosts, notably where aggregations of spores form tissue lesions sometimes leading to post-mortem liquefaction (thus causing significant economic losses to fisheries industries).

TAXON	# spp.	Site	Hosts	Spore		Capsules	
				shape	size	site	size
Order: Multivalvulida (3-13 valves (rarely 2), one polar capsule per valve, all grouped together)							
Family: Trilosporidae (3 valves, 1-3 polar capsules)							
<i>Unicapsula</i>	16	histozoic	mar fish	pyramid	5-7	1 apical	na
<i>Trilospora</i>	4	coelozoic	mar fish	pyramid	7-16	3 apical	=
<i>Trilosporoides incertae sedis</i>	1	coelozoic	mar fish	triangular	24 x 9	3 lateral	≠
Family: Kudoidae (4-13 valves (rarely 2), 4-13 polar capsules, rarely more)							
<i>Kudoa</i>	141	histozoic	mar fish	stellate	7-15	apical	≠
Family: Spinavaculidae (4 valves, 4 polar capsules)							
<i>Octospina</i>	1	coelozoic	fw fish	spindle		apical	=
Order: Bivalvulida (considered in separate section)							

The genus *Trilospora* is characterized by the formation of pyramidal (triradiate) myxospores with 3 valves and 3 apical polar capsules. Four species have been described in the muscles and gall bladders of marine fish. The genus *Trilosporoides* contains a single species forming triangular spores with 3 valves and 3 lateral polar capsules in the gall bladders of marine fish. The genus *Unicapsula* forms small pyramidal spores with 3 unequal valves and one well-developed apical polar capsule. Some 16 species have been reported in the muscles of marine fish, sometimes in association with unsightly lesions which reduces the marketability of infected fish. The genus *Octospina* contains a single species which forms ovoid myxospores with 4 valves, 4 polar capsules and 8 long spines in the gall bladder and swim bladder of freshwater fish. The genus *Kudoa* has traditionally been defined as forming stellate spores with 4 valves and 4 polar capsules within the tissues of marine fish from most oceans around the world. Over 140

species have been described mainly in wild-caught fish, but some have recently been found in fish species being developed for mariculture. Infections have been linked to serious economic losses to the fishing industry as the parasites may cause muscle lesions, neurological or cardiac signs, and post-mortem myoliquefaction (soft flesh, milky condition, jellied meat) in commercially-important species. While many *Kudoa* spp. appear to be highly host specific, several have more extensive host ranges, and their distributions appear to reflect that of their hosts. More recently, morphological, biological and molecular studies have indicated that some widespread species may actually comprise species-complexes and that the genus should be expanded to include several other genera with more complex morphotypic characters; notably genera that form myxospores with > 4 valves and > 4 polar capsules (including *Pentacapsula* (with 5), *Hexacapsula* (with 6), and *Septemcapsula* (with 7)). The life-cycles of multivalvulid species remain to be determined but, like bivalvulid myxosporeans, they are thought to involve actinospore stages in annelids (presumably marine polychaetes), even though some species may undergo direct fish-to-fish myxospore transmission.

Parasite species	Spore dimensions* (µm)	Hosts	Location [clinical signs]	Distribution
*Dimensions are given as length x breadth (and thickness if available) with ranges (or means) expanded to include different populations or subspecies. Measurements given for spores with caudal or lateral processes include those processes (while measurements without processes are given in parentheses).				
Order MULTIVALVULIDA (radially symmetrical spores with 3-13 valves (rarely 2), each with a polar capsule)				
Family Trilosporidae (spores with 3 valves and 3 polar capsules)				
Genus <i>Trilospora</i> (spores appear as triradiate stars with rounded points, apical polar capsules)				
<i>T. californica</i> [type species]	7.2 x 16	marine Blenniiformes: clinid (spotted kelpfish, striped kelpfish); Gobiiformes: oxudercid (blind goby)	gall bladder	North America
<i>T. minuta</i>	5-6-6.3 x 3.2-3.9	marine Gadiformes: macrourid (rock grenadier)	gall bladder wall	North Atlantic
<i>T. muscularis</i>	6.7-9.8 x 5.2-6.6	marine Gadiformes: lotid (blue ling)	muscles	North Atlantic
<i>T. sphaerica</i>	5.4-6 x 5.4-6	marine Gadiformes: morid (longfin codling)	muscles	Alaska
Genus <i>Trilosporoides incertae sedis</i> (spores with conical posterior end, lateral polar capsules)				
<i>T. platessae</i>	24 x 9	marine Pleuronectiformes: pleuronectid (European plaice)	gall bladder	North Atlantic
Genus <i>Unicapsula</i> (syn. <i>Pileispora</i> , <i>Parapileispora</i>) (subspherical spores, 3 unequal valves, one well-developed polar capsule and sometimes 2 reduced 'rudimentary' polar capsules, exclusively histozoic)				
<i>U. aequilobata</i>	6.7-8.5 x 7.1-8.8	marine Carangiformes: carangid (Japanese scad)	muscles [pseudocysts]	Asia
<i>U. andersenae</i>	4.6-7 x 4.3-6.5	marine/estuarine Acanthuriformes: lobotid (broadbanded velvetfin), sciaenid (Japanese meagre, tigertooth croaker, silver white croaker, donkey croaker, Boeseman croaker); Perciformes: gerreid (whipfin silver biddy), lutjanid (Russell's snapper), polynemid (fourfinger threadfin); Pleuronectiformes: cynoglossid (speckled tonguesole); Spariformes: sparid (yellowfin bream), sillaginid (sand whiting); Tetraodontiformes: monacanthid (Japanese leatherjacket)	muscles [pseudocysts]	Australia, China, Vietnam
<i>U. chirocentrusi</i>	6-6.9 x 6-6.9	marine/estuarine Clupeiformes: chirocentrid (dorab wolf-herring)	muscles	India
<i>U. fatimae</i>	5.5-6.6 x 6.1-7.4	marine Perciformes: siganid (white-spotted spinefoot)	muscles	Arabian Sea
<i>U. galeata</i>	5-6.7 x 5-6.5	marine Clupeiformes: dorosomatid (blacktip sardinella), engraulid (common hairfin anchovy, Hamilton's thryssa); Perciformes: mullid (whitesaddle goatfish); Spariformes:	muscles	Indian Ocean

		nemipterid (forktailed threadfin bream)		
<i>U. marquesi</i>	6.1 x 7.2	marine Perciformes: polynemid (giant African threadfin)	gills	Africa
<i>U. maxima</i>	10-14 x 9-11	marine Acanthuriformes: sciaenid (Ganges jewfish)	kidney	India
<i>U. motomurai</i>	6.1-7.5 x 6.1-7.4	marine Perciformes: polynemid (royal threadfin)	muscles	Africa
<i>U. muscularis</i> [type species]	5.8-7.6 x 6.3-7.8	marine Pleuronectiformes: pleuronectid (Pacific halibut, arrowtooth flounder)	muscles [‘wormy halibut’]	Pacific
<i>U. pacifica</i>	7.3-8.6	marine Gadiformes: macrourid (giant grenadier)	muscles	Pacific
<i>U. plugfelderi</i>	4-6.9 x 5.3-6.7	marine Perciformes: mullid (West African goatfish); Spariformes: sparid (picarel, sand steenbras)	muscles	Europe, Africa
<i>U. pyramidata</i>	4.7-6.8 x 5-9.6	marine Eupercaria: nemipterid (monogrammed monocle bream, forktailed threadfin bream, Japanese threadfin bream)	muscles [pseudocysts]	India, China, Vietnam
<i>U. schulmani</i>	7.8-10.3	marine Gadiformes: macrourid (giant grenadier)	urinary bladder	Pacific
<i>U. seriolae</i>	5.2-7.4 x 6.3-7.4	marine Carangiformes: carangid (yellowtail amberjack, yellowstripe scad, greater yellowtail); Perciformes: serranid (Malabar grouper, Japanese grouper); Spariformes: sparid (pink snapper)	muscles [pseudocysts, myoliquefaction]	Australia, Asia
<i>U. setoensis</i>	5.6-6.9	freshwater/estuarine Gobiiformes: oxudercid (yellowfin goby)	muscles	Japan
<i>U. trigona</i>	4.4-5.3 x 5.8-7.8	marine Spariformes: nemipterid (golden threadfin bream)	muscles	Asia
Family Kudoidae				
(spores with 4-13 valves (rarely 2), 4-13 polar capsules)				
Genus Kudoa (syn. <i>Neochloromyxum</i> , <i>Tetraspina</i> , <i>Pentacapsula</i> , <i>Hexacapsula</i> , <i>Septemcapsula</i>)				
(ovoid-quadrangle-stellate spores, histozoic in marine/estuarine fishes, 4 polar capsules unless otherwise stated)				
<i>K. aburakarei</i>	6.4-8.3 x 13.2-18.3 x 13.2-16.6	marine Pleuronectiformes: pleuronectid (arrowtooth flounder)	muscles [pseudocysts]	Alaska
<i>K. acentrogobia</i>	4.2-5.3 x 6-6.7 x 5.1-5.9	freshwater/estuarine Gobiiformes: gobiid (greenspot goby)	muscles [pseudocysts]	China Sea
<i>K. aegyptia</i>	9.1-11.4 x 7.1-8.5 x 3.2-5.9	marine Eupercaria: sparid (Haffara seabream)	heart	Egypt
<i>K. aequidens</i>	2.9-3.5 x 6.2-7.1	freshwater Cichliformes: cichlid (carazinho)	muscles [pseudocysts]	South America
<i>K. ajurutellus</i>	6-7.4 x 7.8-9.5	marine Siluriformes: ariid (Bressou sea catfish)	muscles	Brazil
<i>K. akihittoi</i>	5.3-7 x 9.1-12.5 x 6.8-9.4	marine/estuarine Gobiiformes: gobiid (hazekuchi)	muscles [pseudocysts]	Japan
<i>K. alliaria</i>	6.3-8 x 6.3-10 x 6-10	marine Gadiformes: gadid (southern blue whiting), macruronid (Patagonian grenadier); Perciformes: nototheniid (black rockcod, longtail southern cod)	muscles [pseudocysts]	Southern Atlantic
<i>K. amamiensis</i>	4.5-5 x 5-6 x 5-6	marine Acropomatiformes: pempherid (ypsilon bullseye); Carangiformes: carangid (Japanese amberjack, greater amberjack, bigeye trevally); Perciformes: pomacentrid (scissortail sergeant, Bengal sergeant, Whitley’s sergeant, Indo-Pacific sergeant, stout chromis, pearlspot chromis, blue damselfish)	muscles) [cysts, muscular kudoasis]	Japan, Australia
<i>K. amazonica</i>	5.0-5.9 x 6.3-7.4 x 7.0-7.9	freshwater Siluriformes: pimelodid (mapara)	oesophageal muscles	Brazil

<i>K. anatolica</i>	3.5-4.1 x 6.7-7.2 x 5.3-6	marine Atheriniformes: atherinid (Mediterranean sand smelt)	muscles, urinary bladder, kidney	Black Sea
<i>K. atropi</i>	8-11 x 8-11.9 x 8-9.5	marine Carangiformes: carangid (cleftbelly trevally)	gills [cysts]	India
<i>K. azevedoi</i>	3-4.2 x 4-5.2 x 3.3-4.8	marine Carangiformes: carangid (Atlantic horse mackerel)	ovaries	Tunisia
<i>K. azoni</i>	5-6 x 6.2-7.2 x 5.2-6	marine Scorpaeniformes: hexagrammid (Arabesque greenling, masked greenling)	muscles	Japan
<i>K. barracudai</i>	4.5-5.5 x 5-6	marine Istiophoriformes: sphyraenid (military barracuda)	muscles	Saudi Arabia
<i>K. bengalensis</i>	7-8.5 x 7-11	marine Siluriformes: ariid (flatmouth sea catfish)	muscles	India
<i>K. boopsi</i>	4-6 x 8-10 x 7-8	marine Spariformes: sparid (bogue)	gills [cysts]	Senegal
<i>K. bora</i> (syn. <i>Chloromyxum</i>)	8-9.4 x 9.6-12 x 8.7-12	marine Mugiliformes: mugilid (flathead grey mullet, keeled mullet, long-finned mullet)	muscles [cysts]	Taiwan
<i>K. borimiri</i>	3.3-4 x 4.1-6 x 2.8-4.2	marine Mugiliformes: mugilid (longarm mullet, longfinned mullet)	muscles	Vietnam
<i>K. branchiata</i>	3.8-4.8 x 4.3-4.8 x 4.3-4.8	marine Acanthuriformes: sciaenid (spot croaker)	gills [cysts]	Gulf of Mexico
<i>K. camarguensis</i>	4.4-6 x 6.4-8 x 4.4-6	freshwater/estuarine Gobiiformes: gobiid (common goby, sand goby)	muscles [pseudocysts, myoliquefaction]	France
<i>K. carcharhini</i>	7.2-9.5 x 9.5-11.3 x 7.8-10.6	marine Carcharhiniformes: carcharhinid (nervous shark, pigeye shark, blacktip shark)	muscles	Australia
<i>K. cascasia</i>	6-8 x 7-9 x 7-8	freshwater Mugiliformes: mugilid (yellowtail mullet); Siluriformes: pimelodid (spotted pim)	intestinal mesentery [cysts]	India
<i>K. caudata</i>	5.3-6.7 x 7.9-8.6 x 6.6	marine Scombriformes: scombrid (chub mackerel)	muscles	Peru
<i>K. cerebralis</i>	4.8-5.8 x 5.8-7.2 x 4.8-5.8	marine Moroniformes: moronid (striped bass)	neural connective tissues [cysts]	North America
<i>K. chaetodoni</i>	7.8-10.9 x 15.5-18.3 x 14.0-17.1 [7-9 polar capsules]	marine Perciformes: caesionid (redbelly yellowtail fusilier), chaetodontid (teardrop butterflyfish)	brain [pseudocysts]	Australia
<i>K. cheilodipteri</i>	4.9-7 x 8.3-12.3 x 5.8-7.4	marine Kurtiformes: apogonid (five-lined cardinalfish, yellow-striped cardinalfish, ring-tailed cardinalfish)	muscles	Australia
<i>K. chilkaensis</i>	5.5 x 7.2 x 5.8	marine Beloniformes: belonid (spottail needlefish)	muscles, peritoneum [cysts]	India
<i>K. ciliatae</i>	5-6.3 x 4.7-6.2 x 6.3-7.8	marine Gadiformes: gadid (sand whiting)	intestinal wall [cysts]	Australia
<i>K. clupeidae</i> (syn. <i>Chloromyxum</i>) [type species]	4-5.5 x 5-7.8 x 5.5-6.5	marine Clupeiformes: alosid (Atlantic menhaden, alewife, blueback herring, hickory shad), clupeid (Atlantic herring); Labriformes: labrid (cunner); Perciformes: pomatomid (bluefish); Pleuronectiformes: scophthalmid (common topknot); Scombriformes: scombrid (Atlantic bluefin tuna); Scorpaeniformes: zoarcid (ocean pout); Spariformes: sparid (scup)	muscles [pseudocysts, myoliquefaction]	Atlantic
<i>K. coibori</i>	6-7 x 7.5-8.5 x 8.5-9.8	marine Acanthuriformes: sciaenid (Ganges jewfish)	gut wall	India
<i>K. cookii</i>	5.4-7.8 x 7.6-10	Marine Kurtiformes: apogonid	intestinal	Australia

	x 6.4-9.5	(blackbanded cardinal)	submucosa [cysts]	
<i>K. corniculata</i>	7.5-9.1 x 11-14.8 x 9-11.1	marine Perciformes: leiognathid (Jones' ponyfish, common ponyfish)	muscles [pseudocysts]	China Sea
<i>K. crenimugilis</i>	7-9 x 7-8 x 5-6	marine Mugiliformes: mugilid (fringelip mullet)	intestinal wall	Red Sea
<i>K. cruciformum</i> (syn. <i>Neochloromyxum</i>)	7-9.1 x 6.3-18.2 x 13.6-18.2	marine Perciformes: lateolabracid (Japanese sea bass)	muscles [myoliquefaction]	Japan
<i>K. crumena</i>	6.8-8.2 x 9.3-10.4 x 8.2-9.7	marine Scombriformes: scombrid (Spanish mackerel, yellowfin tuna)	muscles [cysts]	North America
<i>K. cutanea</i> (syn. <i>Pentacapsula</i>)	5.3-6.5 x 12-13.3 x 7.8 [5 polar capsules]	marine Ophidiiformes: carapid (pearlfish)	skin	South Atlantic
<i>K. cynoglossi</i>	5.8-6.5 x 13.8-14.4 x 10-10.6	marine/estuarine Pleuronectiformes: cynoglossid (Senegalese tonguesole)	muscles [cysts]	Nigeria
<i>K. decapterus</i> (syn. <i>Tetraspina</i>)	28.8-43.3 x 30.5-50.7	marine Carangiformes: carangid (Japanese scad)	muscle	China Sea
<i>K. diana</i>	4.5-5.5 x 5.5-6.5 x 5.5-6.5	marine Tetraodontiformes: tetraodontid (bullseye puffer)	oesophagus, intestines [macro-lesions]	Mexico
<i>K. dicentrarchi</i> (syn. <i>Sphaerospora dicentrarchi p.p.</i>)	3.5-6 x 3.5-4 x 4.6-8	marine Moroniformes: moronid (European seabass)	gallbladder wall, intestines	Europe
<i>K. eleotrisi</i>	5.5-8	freshwater Gobiiformes: butid (kongontorkkuja)	gills [cysts]	Africa
<i>K. empressmichikoe</i>	5.1-6.1 x 9.2-11.8 x 6.2-9.1	marine/estuarine Gobiiformes: gobiid (hazekuchi)	muscles [pseudocysts]	Japan
<i>K. encrasicoli</i>	5.8-7.5 x 9.1-12.3 x 5.8-7.4	marine Clupeiformes: engraulid (European anchovy)	muscles	Mediterranean
<i>K. eugerres</i>	4.5-6 x 2.7-3.2 x 3.8-4.7 [2 polar capsules]	marine Eupercia: gerreid (Brazilian mojarra)	gall bladder wall	South America
<i>K. fujitai</i>	4.3-5 x 5.4-6.5 x 5.1-5.8	marine Mugiliformes: mugilid (long-finned mullet)	muscles [pseudocysts]	China Sea
<i>K. funduli</i> (syn. <i>Chloromyxum</i>)	5.1-7.5 x 6.6-7.4 x 4.3-5	marine/estuarine Cyprinodontiformes: fundulid (mummichog)	muscles, fins [pseudocysts, post-mortem myoliquefaction]	North America
<i>K. guangdongensis</i>	13.8-17.1 x 23-46.6 x 9.2-13.3	marine Clupeiformes: dorosomatid (dotted gizzard shad)	muscles [pseudocysts]	China Sea
<i>K. grammatorcyni</i>	6.3-6.7 x 8-9 x 7.6-8.7 [6 polar capsules]	marine Kurtiformes: apogonid (southern orange-lined cardinal fish); Ovalentaria: pomacentrid (scissortail sergeant, blackspot sergeant, blue green damselfish, monarch damsel, black damsel, whitetail damsel, sapphire devil, banded humbug); Scombriformes: scombrid (shark mackerel)	muscles	Australia
<i>K. gunterae</i>	5-6 x 9.3-10.6 x 5.1-5.9	marine Kurtiformes: apogonid (southern orange-lined cardinal fish); Ovalentaria: pomacentrid (scissortail sergeant, banded sergeant, blackspot sergeant, blue green damselfish, sapphire devil, banded humbug, monarch damsel, bowtie damselfish, singlebar devil, whitetail damsel)	muscles	Australia
<i>K. haridasae</i>	4-5.5 x 9-11	marine/estuarine Mugiliformes: mugilid (goldspot mullet)	gall bladder	India
<i>K. hemiscylli</i>	6.9-9.9 x 9-11 x 7.7-10.5 [occasionally]	marine Myliobatiformes: dasyatid (estuary stingray, Kuhl's maskray, bluespotted ribbontail ray);	muscles	Australia

	with 5 polar capsules]	Rhinopristiformes: glaucostegid (common shovelnose ray), rhinobatid (eastern shovelnose ray); Orectolobiformes: hemiscylliid (epaulette shark), orectolobid (western wobbegong, spotted wobbegong, ornate wobbegong)		
<i>K. hexapunctata</i>	6.6-8.3 x 8.9-12.4 x 6.5-10.9 [5-6 polar capsules]	marine Scombriformes: scombrid (Pacific bluefin tuna, yellowfin tuna, longtail tuna)	muscles [myoliquefaction]	Japan, Philippines
<i>K. hirsuta</i>	6.2-8 x 8.7-10.9 x 7.2-9.3	marine Carangiformes: carangid (Japanese jack mackerel, Japanese scad, shortfin scad)	muscles [pseudocysts]	China Sea
<i>K. histolytica</i> (syn. <i>Chloromyxum histolyticum</i>)	12-15 x 5-9	marine Scombriformes: scombrid (Atlantic mackerel); Salmoniformes: salmonid (Atlantic salmon)	muscles, gut, kidney [postmortem myoliquefaction, milky salmon]	Atlantic, Mediterranean
<i>K. hoffmani</i>	10-13 x 8-10.5 x 11-13.5	marine Siluriformes: ariid (roughback sea catfish)	gall bladder	India
<i>K. hypoepicardialis</i>	6.5 x 9.3-11.2 x 7.4-9.3	marine Acanthuriformes: sciaenid (black drum); Carangiformes: carangid (blue runner); Perciformes: lutjanid (northern red snapper), pomatomid (bluefish), serranid (Warsaw grouper); Scombriformes: nomeid (bluebottle fish); Spariformes: lobotid (Atlantic tripletail)	heart	North America
<i>K. igami</i>	5.6-8.2 x 9.2-12.7 x 8.5-9.6 [5-9 polar capsules]	marine Labriformes: labrid (yellowtail wrasse, pastel ringwrasse), scarid (starry-eye parrotfish, Japanese parrotfish)	muscles [pseudocysts]	Japan
<i>K. igori</i>	4.2-4.6 x 4.6-6.5 x 3.5-5.1	marine Mugiliformes: mugilid (longarm mullet)	gall bladder	Vietnam
<i>K. iidae</i>	6-7 x 8.6-12.3 x 7-8.9	marine Perciformes: polynemid (royal threadfin)	muscles [pseudocysts]	Atlantic
<i>K. inornata</i>	5.3-5.5 x 5.8-6 x 5.9-6.1	marine Acanthuriformes: sciaenid (spotted seatrout)	muscles [dystrophic muscle disease]	North America
<i>K. insolita</i>	4.2-5.3 x 6.4-7.5 x 5.3-6.4	marine Carangiformes: carangid (greater amberjack)	muscles [cysts]	Europe
<i>K. intestinalis</i>	3-3.5 x 6.3-7 x 5.8-6.5	marine/estuarine Mugiliformes: mugilid (striped mullet)	intestinal musculature	Japan
<i>K. islandica</i>	4.1-6.8 x 6.5-9.5 x 5-8	marine Scorpaeniformes: anarhichadid (Atlantic wolffish, spotted wolffish), cyclopterid (lumpfish)	muscles	Atlantic
<i>K. iwatai</i>	5-9.5 x 6-11.1 x 5-10.7	marine Acanthuriformes: chaetodontid (Eritrean butterflyfish); Beloniformes: hemiramphid (Red Sea halfbeak); Centrarchiformes: oplegnathid (spotted knifejaw, striped beakfish); Eupercaria: priacanthid (moontail bullseye), sparid (soldier bream, goldlined seabream); Kurtiformes: apogonid (flower cardinalfish); Moroniformes: moronid (European seabass); Mugiliformes: mugilid (flathead grey mullet); Ovalentaria: pomacentrid (threespot dascyllus, Miry's demoiselle); Perciformes: lateolabracid (Japanese sea bass), siganid (marbled spinefoot); Scorpaeniformes: platycephalid	intermuscular, adipose tissue [cysts]	Japan, Israel

		(unspecified flathead); Spariformes: lethrinid (spangled emperor, slender emperor), sparid (black porgy, red porgy, gilthead seabream)		
<i>K. javaensis</i>	4.6-6.3 x 6.2-7.9 x 5.1-7.2	marine Carangiformes: carangid (shrimp scad)	muscles [pseudocysts]	Indonesia
<i>K. kabatai</i>	4-5 x 5-7.7 x 5-7.7	marine Pleuronectiformes: scophthalmid (turbot, common topknot)	muscles [pseudocysts]	North Sea
<i>K. kalae</i>	9.5 x 10.5 x 11.2	marine/estuarine Siluriformes: ariid (threadfin sea catfish)	gall bladder	India
<i>K. kenti</i>	5.1-6.1 x 8.4-9.1 x 7-7.6 [occasionally 5 polar capsules]	marine Ovalentaria: pomacentrid (fire clownfish, Barrier Reef anemonefish, white damsel, singlebar devil)	muscles	Australia
<i>K. konishiae</i>	7.1-8.8 x 8.1-9.7 x 7.1-8.8 [6 polar capsules]	marine Scombriformes: scombrid (Japanese Spanish mackerel)	muscles [pseudocysts]	Japan
<i>K. lateolabracis</i>	5.4-6.9 x 9.9-12.9 x 5.9-9.9	marine Labriformes: scarid (Japanese parrotfish); Perciformes: lateolabracid (unspecified seabass); Pleuronectiformes: paralichthyid (olive flounder)	muscles	Japan
<i>K. leiostomi</i>	6.8 x 8-9.8 x 5.8-7	marine Acanthuriformes: sciaenid (spot croaker)	muscles [pseudocysts, dystrophic muscle disease]	North America
<i>K. lemniscati</i>	9.1-9.5 x 14.1-16.6 x 13.1-16.5 [7-8 polar capsules]	marine Perciformes: lutjanid (yellow streaked snapper)	brain	Australia
<i>K. leptacanthae</i>	2.4-7.2 x 7.2-9.6 x 6-8	marine Kurtiformes: apogonid (threadfin cardinalfish, fragile cardinalfish)	pericardial cavity [pseudocysts]	Australia
<i>K. lethrini</i>	4.5-9.3 x 10.1-12.4 x 9.4-11.9 [6-7 polar capsules]	marine Eupercaria: lethrinid (collared large-eye bream, thumbprint emperor)	brain	Australia
<i>K. longichorda</i>	4.3-5.5 x 6-6.8 x 4.8-6.3	marine Carangiformes: carangid (roughear scad, shortfin scad)	muscles [pseudocysts]	Philippines
<i>K. lunata</i>	4.5-6.2 x 9-11.4	marine Pleuronectiformes: bothid (imperial scaldfish, Mediterranean scaldfish, Thor's scaldfish)	muscles [pseudocysts]	Mediterranean
<i>K. lutjanus</i>	6.3-8.4 x 8.8-10.3 x 7.4-9.8	marine/estuarine Eupercaria: gerreid (saddleback silver biddy), lutjanid (crimson snapper), sparid (yellowfin seabream); Ovalentaria: ambassid (estuary glassfish)	brain, eyes, muscles, swim bladder, serosa, organs [pseudocysts]	Taiwan
<i>K. megacapsula</i>	7.9-15.4 x 10.8-12.9 x 25.5-44.7	marine Carangiformes: carangid (Japanese amberjack), sphyraenid (red barracuda)	muscles [pseudocysts, myoliquefaction]	China
<i>K. miniauriculata</i>	4.9-5.8 x 7-8.5	marine Perciformes: sebastid (Bocaccio rockfish, green striped rockfish)	muscles [pseudocysts]	North America
<i>K. minithyrsites</i>	4.3-5.4 x 7.7-9.9 x 5.8-6.8	marine Acropomatiformes: pempherid (ypsilon bullseye)	muscles [pseudocysts]	Australia
<i>K. mirabilis</i>	6.6-8.8 x 10.3-10.4 x 8.1-12	marine/estuarine Scombriformes: trichiurid (largehead hairtail)	muscles [pseudocysts, myoliquefaction]	Yemen
<i>K. miyakoensis</i>	8.2-11.3 x 12.2-15.6 x 11.2-15.1 [7-8 polar	marine Acanthuriformes: acanthurid (bluespine unicornfish)	brain [pseudocysts]	Japan

	capsules]			
<i>K. monodactyli</i>	7.3-9.2 x 7.7-9.1 [5 polar capsules, occasionally 4-10]	marine Eupercaria: monodactylid (silver moony)	muscles [pseudocysts]	Australia, Vietnam
<i>K. muscularis</i> (syn. <i>Pentacapsula</i>)	7.5-12 x 5-8 x 4.5-6 [5 polar capsules]	marine Acanthuriformes: chaetodontid (redtail butterflyfish)	muscles [cysts, postmortem myoliquefaction]	Philippines
<i>K. musculoliquefaciens</i> (syn. <i>Chloromyxum</i>)	5.3-8.1 x 7.4-10.3 x 7-10	marine Carangiformes: istiophorid (Indo-Pacific sailfish), xiphiid (swordfish)	muscles [pseudocysts, flesh jellification]	Japan
<i>K. neothunni</i> (syn. <i>Hexacapsula</i>)	5.3-8.9 x 9.1-13 x 6.8-12 [6-7 polar capsules]	marine Scombriformes: scombrid (yellowfin tuna, longtail tuna, northern bluefin tuna)	muscles [jellied tuna]	Japan
<i>K. neurophila</i> (syn. <i>Pentacapsula</i>)	8.6-10.3 x 6.8-8 [4-5 polar capsules]	marine Carangiformes: carangid (yellowtail amberjack); Perciformes: latrid (striped trumpeter)	brain [meningo-encephalo-myelitis, scoliosis]	Australia
<i>K. niluferi</i>	5.7-6.1 x 8.8-9.5 x 7-8.1	marine Gobiiformes: gobiid (round goby)	muscles	Black Sea
<i>K. nova</i>	3.1-7.7 x 4-9.8 x 4-6.8	marine/estuarine Carangiformes: carangid (Atlantic horse mackerel, Cape horse mackerel); Gobiiformes: gobiid (round goby, black goby, grass goby, longtail dwarf goby, toad goby, marbled goby, monkey goby, ratan goby, mushroom goby, sand goby, syrman goby, tubenose goby, flatsnout goby, Pinchuk's goby); Eupercaria: sparid (large-eye dentex); Perciformes: pomatomid (bluefish); Scombriformes: scombrid (little tunny, bigeye tuna); Spariformes: sparid (Spanish seabream)	muscles [pseudocysts]	Atlantic, Mediterranean, Black Sea
<i>K. orbicularis</i>	3.6-5 x 4.2-5.8	freshwater Cichliformes: cichlid (acara tucuma)	muscles	Brazil
<i>K. ocellatus</i>	4.5-4.8 x 6.2-7.2	freshwater Cichliformes: cichlid (oscar)	muscles	Brazil
<i>K. ogawai</i>	8.3-9.6 x 12-14.2 x 9.7-11.7	marine Pleuronectiformes: paralichthyid (olive flounder); Scombriformes: scombrid (Pacific barrelfish)	muscles [cysts]	Japan
<i>K. ovivora</i>	5-7.5 x 6.7-8.3 x 5.8-7.7	marine Eupercaria: scarid (redband parrotfish, redfin parrotfish); Labriformes: labrid (bluehead wrasse, yellowhead wrasse, blackear wrasse, slippery dick)	ovaries [reduced fecundity]	Panama
<i>K. pagrusi</i>	6.5-8.6 x 5.8-7.2 x 5.8-7.2	marine Eupercaria: sparid (red porgy)	heart [cysts]	Suez
<i>K. paniformis</i>	4.5-6 x 6-7 x 5-6.5	marine Gadiformes: merlucciid (North Pacific hake)	muscles [pseudocysts, mushy texture]	Canada
<i>K. paralichthys</i>	4.6-6 x 7.4-8.9 x 6.3-7.7	marine Pleuronectiformes: paralichthyid (olive flounder)	brain	Korea
<i>K. paraquadricornis</i>	7.6-8.6 x 12.2-13.9 x 6.6-7.8	marine Carangiformes: carangid (giant trevally, barcheek trevally, brassy trevally, bigeye trevally)	muscles	Australia
<i>K. parathyrsites</i>	8.1-10.9 x 14-16.8 x 9.7-13.3	marine Tetraodontiformes: monacanthid (black scraper)	muscles	Japan
<i>K. parvibulvosa</i>	4.6-6.4 x 6.3-7.2 x 5.7-6.7	marine Carangiformes: carangid (torpedo scad)	muscles [pseudocysts]	China Sea

<i>K. pericardialis</i>	4-4.2 x 6-7 x 4.5-5	marine Carangiformes: carangid (Japanese amberjack)	pericardial cavity [pericardial kudoasis]	Japan
<i>K. permulticapsula</i>	4.6-6.5 x 8.4- 9.9 x 6.3-8.3 [13-15 polar capsules]	marine Scombriformes: scombrid (narrow-barred Spanish mackerel)	muscles [pseudocysts]	Australia
<i>K. peruvianus</i> (syn. <i>K. hallado</i>)	4.6 x 5.5-6.5	marine Gadiformes: merlucciid (Peruvian hake)	muscles [cysts, postmortem myoliquefaction]	Peru
<i>K. petala</i>	5.5-8 x 8.5-11.2 x 6.8-10.2	marine Eupercaria: sillaginid (silver sillago)	gall bladder wall [cysts]	Japan
<i>K. pleurogrammi</i>	4.8-6.8 x 6.7- 9.1 x 5.6-8.2	marine Scorpaeniformes: hexagrammid (Atka mackerel, Okhotsk Atka mackerel)	muscles	Japan, Alaska
<i>K. prunusi</i>	6.7-8.6 x 8.5- 10.3 x 6.7-8.6 [5-6 polar capsules]	marine Scombriformes: scombrid (Pacific bluefin tuna)	brain [pseudocysts, gliosis]	Japan
<i>K. pyramidalis</i>	4.9-6 x 7.1-8 x 6-7.2	marine Carangiformes: carangid (shrimp scad)	gall bladder	China
<i>K. quadratum</i> (syn. <i>Chloromyxum</i>)	5-7 x 5	marine Blenniiformes: blenniid (tompot blenny); Callionymiformes: callionymid (common dragonet); Carangiformes: carangid (Atlantic horse mackerel); Labriformes: labrid (Mediterranean rainbow wrasse); Mugiliformes: mugilid (flathead grey mullet); Scombriformes: scombrid (unspecified mackerel); Scorpaeniformes: cottid (shorthorn sculpin); Siluriformes: ariid (white barbel); Syngnathiformes: syngnathid (great pipefish, narrow-snouted pipefish, worm pipefish, snake pipefish)	muscles, kidneys	Atlantic, Indian Ocean, Mediterranean, White Sea
<i>K. quadricornis</i>	7.8-10 x 14- 15.3 x 5.9-8.7	marine Carangiformes: carangid (gold- spotted trevally)	muscles [pseudocysts]	Australia
<i>K. quraishii</i>	5.9-6.3 x 5.3- 5.7	marine Scombriformes: scombrid (Indian mackerel)	muscles	Saudi Arabia
<i>K. ramsayi</i>	8-10.4 x 4.8-8 x 2.8-4.8	marine Perciformes: nototheniid (longtail southern cod)	muscles	Falklands
<i>K. rayformis</i>	5-5.7 x 4.6-5.7 x 6.1-9.2	marine Scombriformes: scombrid (Pacific sierra)	muscles [pseudocysts]	Panama
<i>K. rosenbuschi</i> (syn. <i>Chloromyxum</i>)	6-7 x 6.5 x 5.5	marine Gadiformes: merlucciid (Peruvian hake, Argentine hake)	muscles [myoliquefaction]	Argentina
<i>K. rousseauxii</i>	4.2-6.7 x 6.8- 9.6 x 4-6.9	freshwater Siluriformes: pimelodid (gilded catfish)	muscles	Brazil
<i>K. sagarica</i>	12.5-14 x 10-12 x 8.5-10.5	marine/estuarine Mugiliformes: mugilis (goldspot mullet)	gall bladder	India
<i>K. saudiensis</i>	4.3-5.4 x 3.4- 4.3	marine Scombriformes: scombrid (Indian mackerel)	ovaries	Saudi Arabia
<i>K. schulmani</i> (syn. <i>Pentacapsula</i>)	7-8	marine Spariformes: nemipterid (Japanese threadfin bream)	muscles	Indian Ocean
<i>K. sciaenae</i>	4.8-6.4 x 6.4	marine Acanthuriformes: sciaenid (lorna drum, minor stardrum, louna-tahmkala, Peruvian banded croaker)	muscles [pseudocysts]	Peru
<i>K. scomberi</i>	6.1-6.8 x 8.2- 10.5 x 7-8.8	marine Scombriformes: scombrid (chub mackerel)	muscles [cysts]	Japan
<i>K. scomberomori</i>	5-6.8 x 6.8-8.2 x 6.1-7.6 [6 polar capsules]	marine Scombriformes: scombrid (narrow-barred Spanish mackerel, Indo- Pacific king mackerel)	muscles	Australia, Vietnam
<i>K. sebastea</i>	5.4-5.6 x 7.3- 8.2 x 5-5.5	marine Perciformes: sebastid (petit perch)	muscles	Japan

<i>K. septempunctata</i>	6.8-10.6 x 11.1-16.4 x 8.9-14.8 [5-8 polar capsules]	marine Pleuronectiformes: paralichthyid (olive flounder); Tetraodontiformes: monacanthid (black scarper)	muscles [pseudocysts]	Korea
<i>K. shiomitsui</i>	5.6-7.4 x 6.7-10.3 x 6.7-9.8	marine Pleuronectiformes: paralichthyid (olive flounder); Scombriformes: scombrid (Pacific bluefin tuna); Tetraodontiformes: monacanthid (thread-sail filefish, unicorn leatherjacket), tetraodontid (Japanese puffer)	heart, pericardial cavity [cysts]	Japan
<i>K. shkae</i>	6.1-6.2 x 7-8.1	marine Siluriformes: ariid (hardhead catfish)	muscles	North America
<i>K. sphyraeni</i>	9-10.2 x 9.5-10.5 x 9.5-10.5	marine Istiophoriformes: sphyraenid (pickhandle barracuda)	intestinal wall, muscles [cysts]	India
<i>K. stellula</i>	5-6.9 x 3.7-4	marine Atheriniformes: atherinid (Mediterranean sand smelt)	kidney	Black Sea
<i>K. surabayaensis</i>	4.6-5 x 6.4-7.6 x 5.8-6.7	marine Mugiliformes: mugilid (flathead grey mullet)	muscles [pseudocysts]	Indonesia
<i>K. tachysurae</i>	4.5-6 x 7-9 x 5-6.5	marine Siluriformes: ariid (thinspine sea catfish)	gall bladder	India
<i>K. tetraspora</i>	8-11 x 8-12 x 8-12	marine/estuarine Mugiliformes: mugilid (striped mullet)	muscles, brain, optic lobes [cysts]	India
<i>K. thalassomi</i>	6.1-10.9 x 9.4-16.1 x 8.5-13.8 [6-7 polar capsules]	marine Acanthuriformes: acanthurid (bluespine unicornfish); Labriformes: labrid (moon wrasse), scarid (Japanese parrotfish); Ovalentaria: pomacentrid (Bengal sergeant)	muscles [pseudocysts]	Australia, Japan
<i>K. thunni</i>	6.4-6.6 x 9.2-9.9 x 7.7-9.9	marine Scombriformes: scombrid (albacore, yellowfin tuna)	muscles [cysts]	Japan
<i>K. thyrsites</i> (syn. <i>Chloromyxum</i>)	5.6-9.1 x 6-18.2 x 10.8-19	marine Beloniformes: exocoetid (unspecified flying fish); Beryciformes: berycid (splendid alfonso); Carangiformes: carangid (Indian scad), coryphaenid (mahi-mahi); Clupeiformes: alosid (Australian pilchard, South African pilchard), dorosomatid (Bali sardinella), engraulid (Australian anchovy, Japanese anchovy), spratelloidid (delicate round herring); Gadiformes: gadid (walleye pollock), merlucciid (Cape hake, North Pacific hake, North Pacific hake, Pacific halibut); Perciformes: aulorhynchid (tube-snout), cottid (threadfin sculpin), lateolabracid (Japanese seabass); Pleuronectiformes: paralichthyid (olive flounder), pleuronectid (arrowtooth flounder, Pacific Dover sole, rock sole); Salmoniformes: salmonid (Atlantic salmon, Pacific salmon, coho salmon, brown trout); Scombriformes: gempylid (barracouta), trichiurid (silver scabbardfish); Scorpaeniformes: hexagrammid (lingcod); Tetraodontiformes: monacanthid (black scraper); Zeiformes: zeid (unspecified dory)	muscles [pseudocysts, postmortem myoliquefaction, milky barracouta, pap snoek]	Atlantic, Pacific
<i>K. trachuri</i>	5.5-7.5 x 5.9-8.5 x 4.5-6.2	marine Carangiformes: carangid (Japanese jack mackerel, white trevally, aka-aji, Japanese scad, shortfin scad,	muscles [cysts]	Japan

		roughear scad)		
<i>K. trifolia</i>	13.6-15.4 x 3.3-4 x 13.6-15.5	marine Mugiliformes: mugilid (golden grey mullet, thinlip mullet)	connective tissues, spleen, kidney, intestines, gall bladder, mesenteries, gills	Spain
<i>K. uncinata</i>	5.2-8 x 9.1-13.4 x 5.9-10.8	marine Acanthuriformes: leiognathid (shortnose ponyfish, spotnape ponyfish, orange ponyfish)	muscles [pseudocysts]	China
<i>K. unicapsula</i>	4.7-5.5 x 6.6-8.4 x 4.7-6.9	marine Mugiliformes: mugilid (thinlip mullet, golden grey mullet)	intestines, mesenteries	Spain
<i>K. valamugili</i>	5.2-6.6 x 4.3-5.6 x 5-5.4	marine Mugiliformes: mugilid (longarm mullet)	intestinal muscles	India
<i>K. vesica</i>	5.3-6.6 x 8-9.9 x 8-10.6	marine Scombriformes: centrolophid (southern driftfish)	muscles, urinary bladder	Antarctica
<i>K. viseuensis</i>	7.2 x 5.2	marine Batrachoidiformes: batrachoidid (Pacuma toadfish)	muscles	Asia
<i>K. whippsi</i>	4.2-7.4 x 7.9-15 x 4.7-10.4	marine Kurtiformes: apogonid (southern orange-lined cardinalfish, yellow-striped cardinalfish, ring-tailed cardinalfish, Doederlein's cardinalfish); Mugiliformes: mugilid (longarm mullet, longfinned mullet); Ovalentaria: pomacentrid (Bengal sergeant, Whitley's sergeant, spiny chromis, Barrier Reef anemonefish, fire clownfish, blue green damselfish, bowtie damselfish, whitetail damsel); Perciformes: cheilodactylid (spotted tail morwong)	muscles	Pacific
<i>K. yasai</i>	5.6-7.2 x 7.7-8.6 x 4.2-6	marine Eupercaria: sciaenid (king weakfish)	muscles	Brazil
<i>K. yasunagai</i> (syn. <i>Septemcapsula</i>)	4.3-8.4 x 9.4-14.5 x 7.1-14 [5-8 polar capsules]	marine Acanthuriformes: sciaenid (Japanese meagre); Carangiformes: carangid (Japanese amberjack); Eupercaria: lutjanid (blackspot snapper), nemipterid (monogrammed monocle bream); Labriformes: scarid (Japanese parrotfish); Mugiliformes: mugilid (blackfin mullet); Perciformes: lateolabracid (Japanese seabass), oplegnathid (striped beakfish); Pleuronectiformes: paralichthyid (olive flounder); Scombriformes: scombrid (Pacific bluefin tuna); Tetraodontiformes: tetraodontid (Japanese puffer)	brain [pseudocysts]	Japan
Family Spinavaculidae (4 valves, 4 polar capsules at one pole, iodophilous vacuole)				
Genus <i>Octospina</i> (ovoid to spindle-shaped spores with 8 spines, coelozoic in freshwater fishes)				
<i>O. tongrensis</i> [type species]	12.2-13.5 x 8.5-9.8 x 3.8-4.5	freshwater Cypriniformes: cyprinid (grass carp)	gall bladder, swim bladder	China
Order BIVALVULIDA (two valves meeting in circumspiral suture, 1-4 (usually 2) polar capsules) considered in separate section				
Class: MALACOSPOREA (spores with soft (unhardened) shell valves) considered in previous section				

It has now been demonstrated that some myxosporean parasites have heteroxenous (2-host) life-cycles involving the formation of actinospores in annelid hosts and myxospores in piscine hosts. Early classification schemes placed all actinospores in the order Actinomyxida, characterized by spore bodies containing 3 apical polar capsules (often with protruding tips) and most with 3 long hollow caudal projections which inflated osmotically in water to provide spore buoyancy for dispersal in water currents. Four families were recognized from oligochaetes and sipunculids: Tetractinomyxidae (*Tetractinomyxon*); Sphaeractinomyxidae (*Neoactinomyxum*, *Sphaeractinomyxon*); Triactinomyxidae (*Antonactinomyxon*, *Aurantiactinomyxon*, *Echinactinomyxon*, *Guyenotia*, *Raabeia*, *Siedleckiella*, *Synactinomyxon*, *Triactinomyxon*); and Hexactinomyxidae (*Hexactinomyxon*). However, with the discovery that these stages represent different stages in the life cycles of myxosporean parasites, it was suggested that actinosporean classification be suppressed and that actinospores be assigned to collective groups with vernacular names. To date, some 20 groups have been identified: anton-, auranti-, echin-, hex-, hung-, ormier-, pseudtri-, seis-, sphaer-, syn-, tetra-, tri-, unicapsul-actinomyxon, neoactinomyxum, saccimyxon, endocapsa, guyenotia, raabeia, siedleckiella, and tetraspora (with key characters tabulated below).

Actinospore type	Spore		Polar capsules	Other characters	Hosts
	Body shape	Projections			
antonactinomyxon	ellipsoidal	long, lanceolate, divergent	pyriform (protruding tips)	groups of 8 spores form cuboidal networks	freshwater oligochaetes
aurantiactinomyxon	ellipsoidal	short, stout, curved, leaflike, divergent	pyriform (protruding tips)	spores appear triradiate from above	freshwater oligochaetes
echinactinomyxon	rectangular	straight, tapered, blade-like, divergent	pyriform (slightly protruding)	spores appear stellate	freshwater oligochaetes
endocapsa	subspherical	small, bulge-like caudal swellings	pyriform (not protruding)	spores compact	marine oligochaetes
guyenotia	subspherical	long, stout, blunt, grouped	pyriform (protruding tips)	spores tripod-like	freshwater oligochaetes
hexactinomyxon	rectangular	long, thin, pointed, bifurcate	pyriform (protruding tips)	spores anchor-like	freshwater oligochaetes
hungactinomyxon	subspherical	long, tapering, divergent	rounded (not protruding)	spores form interlaced cuboidal networks	freshwater oligochaetes
neoactinomyxum	subspherical	absent	pyriform (protruding tips)	spores appear triangular from above	freshwater oligochaetes
ormieractinomyxon	ovoid	long, tapering rod, terminal anchors	pyriform (protruding tips)	groups of spores interlock to form chains	freshwater oligochaete
pseudtriactinomyxon	ovoid	long, blade-like, divergent	pyriform (protruding tips)	projections with longitudinal suture	freshwater oligochaetes
raabeia	ellipsoidal	long, tapering, curved, divergent	pyriform (protruding lips)	spores grapplehook-like	freshwater oligochaetes
saccimyxon	saccular	absent	pyriform (not protruding)	spores appear globular	marine polychaetes and sipunculids
seisactinomyxon	rectangular	long, stout, divergent, bifurcate	pyriform (protruding lips)	spores grapplehook-like	freshwater oligochaetes
siedleckiella	ellipsoidal	long, stout, divergent	pyriform (protruding tips)	groups of spores form interlocked mesh	freshwater oligochaetes
sphaeractinomyxon	subspherical	absent	pyriform (not protruding)	spores solid, rounded	freshwater and marine oligochaetes
synactinomyxon	spherical	each valve with one short anterior and 2 long caudal processes	round (not protruding)	spores stellate with sinuous projections	freshwater oligochaetes
tetractinomyxon	pyramidal	absent	pyriform (not protruding)	spores appear triangular	freshwater and marine polychaetes, sipunculids
tetraspora	subspherical	absent	pyriform (not protruding)	spores antero-posteriorly flattened	marine oligochaetes
triactinomyxon	rectangular	long, tapering, pointed, curved	pyriform (protruding tips)	spores anchor-like	freshwater and marine oligochaetes
unicapsulactinomyxon	ovoid	long, thin, pointed, one anterior, 2 posterior	single large polar capsule	polar capsule opens laterally	marine polychaetes

Parasite morphology: Myxozoan parasites are multicellular (sometimes termed 'pluricellular') aquatic parasites that include myxosporeans, actinosporeans and malacosporeans (the latter 2 covered in the preceding bivalvulid section). Myxosporeans develop in vertebrate hosts (mainly fish) where they form 5 different developmental stages: namely, trophozoites, plasmodia, pansporoblasts, sporoblasts and myxospores. The earliest developmental stages are trophic stages which range from the small invasive uninucleate amoebulae (around 10 µm in diameter) to larger multinucleate trophozoites (up to 80-100 µm) which often develop in the same tissues as spore formation (although a few species undergo an 'extrasporogonic' cycle in different tissues). The trophozoites form cell doublets by nuclear division and endogeny whereby secondary daughter cells are formed within vacuoles in primary maternal cells (this enveloped 'cell-in-cell' condition is typical for myxozoa). This generates polymorphic stages in which growth and proliferation of the secondary cells occurs either within host tissues (histozoic) or within body-organ cavities (coelozoic). These stages generally take 3 forms: remaining as small microscopic (~ 10 µm) pseudoplasmodia (usually histozoic) initially containing one vegetative nucleus and producing 1-2 spores; growing to small intermediate (~ 100 µm) plasmodia (usually coelozoic) that are mitosporic producing 1, 2 or more spores; or growing to form large (up to 2-4 mm) plasmodia typically containing many nuclei and specialized cells producing masses of spores. The plasmodia may vary in shape from flat sheet-like to round sac-like to elongate worm-like stages, and large histozoic plasmodia often becoming ensheathed by host connective tissue cells thus forming whitish 'myxosporean' cysts. Some coelozoic species may adhere to cavity walls by developing temporary cytoplasmic holdfast outgrowths (occasionally called pseudopodia). Members of the genera *Kudoa* and *Unicapsula* typically form large polysporic plasmodia within the muscles of fishes (sometimes within cysts), while those of *Trilospora* and *Octospina* are often coelozoic forming smaller plasmodia in organ cavities. Although most myxosporeans species undergo spore formation (sporogenesis) within pansporoblasts (formed when pericytes envelope sporogonic cells), members of the genera *Kudoa* and *Unicapsula* do not form pansporoblasts but rather develop large polysporic plasmodia within which sporogonic cells are capable of producing up to 8 myxospores. Sporogonic cells divide by binary fission giving rise to sporoblast cells that undergo valvogenic, capsulogenic and sporoplasmic differentiation to form hard-shelled myxospores with multiple shell valves joined along suture lines, nematocyst-like polar capsules and amoeboid infective sporoplasms. Conventionally, myxosporean taxonomy has been based on the configuration of the mature spores, with those of multivalvulid species contain 3-13 valves (rarely 2), 1-13 polar capsules (rarely more) and 1-2 sporoplasms, whereas bivalvulid species contain 2 shell valves, 1-4 polar capsules (usually 2), and 1-2 sporoplasms. Most multivalvulid species form spores ranging in size from 4-16 µm with indistinct suture lines, delicate membranous envelopes, apical polar capsules and 2 uninucleate sporoplasms (one sometimes enveloping the other). Amongst the Multivalvulida, members of the family Trilosporidae form spores with 3 valves (*Unicapsula* forming subspherical spores with 1 polar capsule, *Trilospora* forming triradiate spores with 3 polar capsules), while members of the families Kudoidae and Spinacaulidae form spores with 4 valves (*Kudoa** forming rounded, quadrate or stellate spores with 4 polar capsules, *Octospina* forming ovoid to spindle spores with 4 polar capsules and 8 spines). [*Note that recent studies now include spores with 5-13 polar capsules in the genus *Kudoa* rather than the genera *Pentacapsula*, *Hexacapsula* or *Septemcapsula*, with some species even having multiple spore morphotypes within a single plasmodium (e.g. *K. monodactyli* with 5 or more spore valves and polar capsules and *K. permulticapsula* with up to 13 polar capsules)].

Site of infection: Myxosporean infections in vertebrate hosts may be coelozoic (inhabiting cavities) and/or histozoic (within tissues), with developing stages and spores usually found in specific locations (implying strict tissue tropism) although some species are more disseminated throughout their hosts. Coelozoic species are usually found in the gall bladder but can occur in other body/organ cavities (urinary bladder, swim bladder, intestines), whereas histozoic species may infect a variety of tissues and organs (cutis, gills, muscles, central nervous system, cartilage, kidney, liver, and gut wall). Myxospores have been found in freshwater and marine fish around the world, including anadromous species (that migrate from the sea into freshwater to spawn) and catadromous species (that migrate from freshwater into the sea to spawn), as well as those inhabiting brackish and estuarine waters. Over 160 multivalvulid species have been described mainly in marine fish, being reported in over 300 species (belonging to 105 families in 36 orders), while only a dozen species have been recorded in freshwater fish (belonging to 6 families in 5 orders). In comparison, some 2,945 bivalvulid species have been found in 540 species of marine fish (from 211 families in 61 orders), 1,100 species of freshwater fish (from 126 families in 35 orders), 120 amphibian species (90 frog species, 14 toads, 17 urodelans, 1 caecilian), 17 reptile species (testudines), and rarely mammals (2 shrew species) and birds (one duck species).

Pathogenesis: Infections by myxosporean parasites are generally subclinical in nature, even when developing plasmodia and spores may cause some microscopic lesions, but not severe enough to compromise organ/tissue structure/function. Nonetheless, heavier infections by some species, particularly those forming macroscopic lesions, may result in space-occupying lesions with tissue necrosis and/or hypertrophy, fibrotic encapsulation, inflammation and oedema resulting in pressure atrophy, blockages, ischaemia and anoxia that may be progress to become fatal. The extent of damage inflicted on the host depends on many factors, including host susceptibility (due to variations in innate and acquired resistance), parasite aggressiveness (proliferative potential, tissue tropism) and environmental conditions (temporal and spatial variations in climate and habitat). Most coelozoic infections in organ or body cavities are benign although some have been associated with discolourations and partial blockages, mainly in the gall bladder and upper urinary tract. Histozoic infections vary considerably in their effect on the host depending on the organs involved, the intensity of infection and the sizes of the lesions. A growing number of histozoic species have been found to form cysts or pseudocysts causing space-occupying lesions. Some infections in nervous tissues have been associated with behavioural disorders, some in cartilage may produce gross deformities, and some infections in somatic musculature may result in visible unsightly lesions which can undergo post-mortem myoliquefaction affecting fillet quality and economic value.

Despite the prevalence and broad host distribution of infections by *Kudoa* spp., most do not cause significant morbidity or mortality as they are often cleared by host immune responses system within a year. Myxospores are ingested by macrophages and destroyed, followed by the repair of host tissues. Any inflammatory responses are generally coincident with myxospore formation, rather than earlier proliferative stages. Mature plasmodia may become surrounded by dense fibrous capsules formed by host connective tissue cells resulting in cavity-like lesions with cyst or pseudocyst formation. Pseudocysts lack an inner parasite-derived lining, and their formation is followed by necrotic changes with the pseudocyst wall formed by reparative inflammation. It has also been shown that the majority of severe infections take place in immunocompromised animals, and even then do not result in anything more than chronic inflammation. Pre-sporogonic developmental stages do not elicit strong immune responses and encysted sporogonic stages are sequestered away from the host immune system. This state of 'immune evasion' generally last until mature myxospores begin to be released, but the resultant immune responses often only lead to the development of multifocal chronic inflammation between muscle fibres that subsides with tissue repair. While developing stages may exhibit low pathogenic potential, their presence does pose a serious threat to fisheries because the cysts may become macroscopically visible as unsightly whitish spots or streaks in the flesh. The cysts may sometimes exhibit dark discolourations initially thought to be due to melanin deposition but now attributed ultrastructurally to the accumulation of breakdown products. The resultant blemishes are aesthetically unappealing and considerably reduce the market value of the fish. They may also severely compromise product quality by causing postmortem myoliquefaction (soft mushy or milky flesh) due to the release of parasite proteolytic enzymes (including cysteine proteases) when cysts are disturbed by processing (filleting, freezing/thawing, cooking/smoking). It has been suggested that myoliquefaction may be a natural process by which mature myxospores are released from host tissues, as anoxic postmortem tissues undergo anaerobic glycolysis with acidic waste products promoting proteolysis. Myoliquefaction has been reported for several multivalvulid species, including *Kudoa thrysites* in Atlantic salmon and coho salmon, *K. clupeiidae* in Atlantic herring, *K. cruciformum* in seaperch, *K. funduli* in mummichog, *K. histolytica* in mackerel, *K. mirabilis* in ribbonfish, *K. musculoliquefaciens* in swordfish, *K. neothunni* in yellowfin tuna, *K. paniformis* and *K. peruvianus* in hake, *Unicapsula seriola* in amberjack, and *U. muscularis* in halibut. Infections in fish muscles are also thought to occasionally cause food poisoning in humans, with a self-limiting diarrhoeic illness developing after the consumption of traditional sushi or sashimi prepared using raw flesh containing *Kudoa* cysts (e.g. *K. septempunctata* in flounder, *K. hexapunctata* and *K. neothunni* in tuna, *K. iwatai* in bream, and *Unicapsula seriola* in amberjack). Infections in fish may also extend into other tissue and organ systems, including the brain, with several species apparently having little effect (e.g. *K. paralichthys* in olive flounder, *K. tetraspora* in mullet, *K. cerebralis* in striped bass), while others may elicit intense reactions (e.g. *K. neurophila* causing severe granulomatous meningo-encephalo-myelitis in striped trumpeters, *K. yasunagai* forming macroscopic lesions in sea bass and beakfish). One species (*K. ovivora*) was found to reduce the fecundity of wrasse by invading the ovaries and rendering maturing oocytes non-viable. Other species were found to infect the smooth muscle of the intestinal wall, with *K. intestinalis* having little effect on striped mullet, while *K. diana* formed large cysts that occasionally ruptured.

Developmental cycle and mode of transmission: Myxosporeans in fish first undergo vegetative proliferation in pseudoplasmodia or plasmodia followed by myxospore morphogenesis, both processes featuring a characteristic cell-in-cell condition where endogenously produced secondary cells persist inside primary mother cells. Vertebrates become infected when mature actinospores come into contact with external epithelia (skin and/or gills) discharging filaments from their polar capsules to facilitate attachment. The spore shell valves then open releasing the infective germ cells (sporoplasms) which penetrate the epithelial barriers. The sporoplasms are either single binucleate cells (whose nuclei fuse to form a synkaryon) or 2 uninucleate cells (that fuse by autogamy to form a single cell). They transform to trophic stages (trophozoites), initially called amoebulae, as they invade host tissues, often moving deeper via blood or lymph vessels. The trophozoites undergo proliferation by forming cell doublets through nuclear division and endogeny whereby one daughter nucleus becomes enveloped by endoplasmic reticulum cisternae resulting in a secondary cell located within a vacuole in the primary cell (resulting in the enveloped cell-in-cell condition typical for myxozoa). All species undergo sporogonic cycles forming plasmodia (or pseudoplasmodia) involving growth and proliferation of generative secondary cells and vegetative nuclei. These stages are either immobile rounded stages encased in host tissues (histozoic) or occur as flat sheets or rounded balls within body or organ cavities (coelozoic) where they are attached to the walls by cytoplasmic holdfast outgrowths or occur free-floating in the lumina. This plasmodial development is often coupled with sporogony (spore formation) although some species undergo extrasporogonic cycles in tissues other than where sporogony occurs. Extrasporogonic cycles have been reported for members of the genus *Kudoa*, whereby secondary cells undergo a series of mitotic divisions and then endogenous budding to give rise to tertiary cells. The secondary cells are released by rupture of the primary cells allowing parasites to migrate via blood or lymph vessels to their final sites where sporogony occurs. All species undergo plasmodial development that typically involves one or more of three morphological types: numerous small pseudoplasmodia (containing only one vegetative nucleus) that produce 1-2 spores (mono- or di-sporic) often being histozoic (sometimes pervading host tissues as diffuse infiltrates); medium plasmodia that are mictosporic producing 1, 2 or more spores often being coelozoic; and large plasmodia (sometimes macroscopic) that produce masses of spores (poly-sporic) often being histozoic (sometimes encysted by host connective tissue). *Kudoa* and *Unicapsula* spp. are predominantly histozoic typically forming large polysporic plasmodia within the musculature, while *Trilospora* and *Octospina* spp. are usually coelozoic forming smaller plasmodia in organ cavities. Although most myxosporeans species undergo sporogenesis within pansporoblasts (formed when pericytes envelope sporogonic cells), *Kudoa* and *Unicapsula* spp. do not form pansporoblasts but rather directly form sporogonic cells that are capable of producing up to 8 myxospores. The sporogonic cells divide by binary fission giving rise to sporoblast cells that undergo valvogenic, capsulogenic and sporoplasmic differentiation

to form hard-shelled myxospores with multiple shell valves joined along suture lines, nematocyst-like polar capsules and amoeboid infective sporoplasms. Mature myxospores are released into the aquatic environment either by the antemortem rupture of superficial cysts or the postmortem degradation of infected tissues upon the death and decay of the host. Myxospores are highly resilient to external environmental conditions, and some have been shown to retain infectivity for up to 4 months in mud, for 2 months after freezing at -20°C , and even after passage through the alimentary canal of predatory birds and fish. Myxospore infections in fish often show seasonal patterns of infection, with prevalence generally highest in autumn/winter in subtropical regions, or summer/autumn in temperate regions, although patterns can be hard to discern within specific age groups. Epidemiological observations indicate infection prevalence and abundance may vary according to prevailing environmental conditions (notably water temperature and salinity) but also numerous host factors (population density, age cohorts, migratory, breeding, spawning and feeding habits, nutritional, physiological and immunological status). It was initially thought that many myxospore infections in fish were long-lasting (potentially life-long) but there is growing evidence that infections may cycle seasonally with developing stages not persisting longer than one year. Infections generally do not evoke strong host immune responses, so there may be little protective immunity acquired by fish even after repeated exposure.

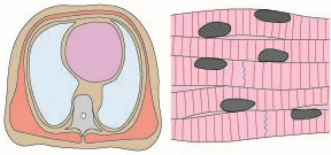
Initially, epidemiological studies suggested that myxospores may be transmitted directly from fish to fish, possibly ascending the food chain when big fish eat little fish, and sometimes with caveats that water-borne spores needed to be 'aged' in sediments to become infective, or passaged through the digestive tracts of aquatic invertebrates. This led to the widespread belief that the feeding of infected 'trash' fish to commercial species may be responsible for disease outbreaks, but direct fish-to-fish transmission has not been substantiated for any multivalvulid species (with the possible exception of *Kudoa ovivora* that infects the eggs of wrasse). It was subsequently discovered experimentally that myxosporeans require a secondary or alternate host to complete their life-cycle. Myxospores from fish were found to be infective for aquatic invertebrates (annelids) where they underwent development and the formation of different types of spores (namely actinospores) that proved to be infective to fish. Development in annelids involved asexual proliferation (merogony) followed by sexual reproduction (gametogony) where the zygotes differentiated into actinospores. By definition, this makes annelids the final or definitive hosts (in which sexual development occurs) and fish should be considered simply as intermediate hosts. Heteroxenous (2-host) life-cycles have now been demonstrated for species within 16 bivalvulid genera (see previous section), but not yet for any multivalvulid genera. Clearly, further studies are required to establish parasite life-cycles and unravel the complexities of transmission.

Differential diagnosis: The diagnosis of myxosporean infections in fish on clinical grounds is presumptive, as other aetiological agents or pathological conditions may cause similar symptoms, signs or behaviours. The observation of macroscopically visible cysts in host tissues is not pathognomic as other infectious agents may cause similar encapsulated lesions, especially bacteria. Most infections are diagnosed at post-mortem by the detection and identification of myxospores recovered from host tissues or organ cavities. Samples are usually examined microscopically as wet mounts, smears, tissue imprints, squash preparations or sections, preferably using high contrast illumination systems (e.g. phase-contrast, differential interference-contrast). Microscopy is best performed on fresh samples, as preservatives and freezing may distort spore integrity (especially size and shape). Nonetheless, high-volume screening studies often make recourse to the examination of histological sections of fixed tissues. A range of stains have been employed to improve visual acuity, including Giemsa and silver stains, and some fluorochromes and biotinylated lectins. Several techniques have also been developed to harvest spores from host tissues by maceration, homogenization, enzymatic digestion (pepsin or trypsin), filtration and/or centrifugation. Parasite genera may be identified by the morphological characteristics of their mature spores (size, shape, structure, sutural ridges, spore projections, caudal appendages, ribs, ridges or striae), polar capsule morphology (number, shape, size and angle, arrangement of coils of the polar filaments, position of capsule opening) and sporoplasms (number, location). Specific differentiation often requires further information on pre-spore developmental stages as well as tissue location, pathological changes, host occurrence and geographic location. Both transmission and scanning electron microscopy may be required to reveal topographical and cellular ultrastructural features. A small range of immunological techniques have also been developed to guide research and aid diagnoses. Monoclonal and/or polyclonal antibodies have been raised against extrasporogonic stages and mature spores of several economically important myxozoan species (including the multivalvulid *Kudoa thyrssites*) and used with variable success to detect parasites within fish tissues or tissue extracts, usually by chemiluminescence. Enzyme immunoassays have also been developed to detect host antibodies against *K. thyrssites* antigens in serum samples, yielding specific and sensitive results which allowed reasonable prediction of the degree of postmortem myoliquefaction that may occur. Modern molecular biological techniques are now commonly used to characterize species and determine phylogenetic relationships following the polymerase chain reaction (PCR) amplification of nuclear (large and small subunit ribosomal RNA and internal transcribed spacer regions) or mitochondrial (cytochrome c oxidase subunit I) genes.

Treatment and control: There are few chemotherapeutic agents that work against multivalvulid myxosporean infections in fish. Some successes were observed treating bivalvulid infections using a range of toxic compounds (including malachite green, acetarsol, and dimetridazole) but none worked against multivalvulid *Kudoa* infections and most have since been withdrawn from commercial use due to concerns over their bioaccumulation and toxicity. Similarly, the use of the antibiotic fumagillin showed little effect against *Kudoa* infections despite good success against some bivalvulid infections. There have been a few reports suggesting that dietary supplementation with the coccidiostat nicarbazin may be effective against *K. thyrssites* in Atlantic salmon, but several problems were encountered with growth retardation, drug residues and some mortalities. Reasonable disease control has been achieved in aquaculture by the adoption of preventive measures designed to minimize the introduction, amplification, survival and

spread of parasites amongst fish stocks, with desirable management procedures often mandated by government and/or industry regulations. Procedures used to minimize the introduction of parasites into culture facilities include health screening all source and translocated stocks, establishing appropriate quarantine procedures, maintaining temporal and spatial records of parasite distribution and abundance, and implementing education and awareness campaigns for producers and consumers. Previous recommendations to curtail the feeding of infected trash fish (e.g. pilchards, sardines) to cultured stock have not been supported by experimental studies nor by molecular characterization studies. Protocols employed to avoid contamination of holding facilities include the prompt removal and destruction of diseased fish (by onshore burial or incineration), regularly cleaning fomites and equipment using chemicals, heat or desiccation, and frequently changing netpens and moving them to deeper waters (thus reducing contact with benthos potentially harbouring annelids). Husbandry practices should strive to keep fish in optimal health as they become more susceptible to infection and disease when stressed. Good management involves maintaining water quality (appropriate temperature, pH, aeration, turbidity, solutes), reducing organic loads (monitoring planktonic and benthic plant and animal communities), providing good nutrition without over-feeding, stocking without over-crowding, avoiding conditions where fish become immunocompromised (by treating concomitant infections, and even removing sexually-mature salmonids as those of some species become partially immuno-suppressed), separating species and age cohorts, harvesting fish before parasite maturation (particularly in colder winter months when prevalence is reduced), and selectively breeding resistant fish (some prospects based on fish species/strain/stock differences in susceptibility for particular infections, especially amongst salmonids). Several studies have also shown that the incidence of post-mortem myoliquefaction can be reduced by implementing post-harvest treatments with potato extracts, egg whites and/or bovine plasma proteins to inhibit parasite proteolytic enzymes released during handling and processing.

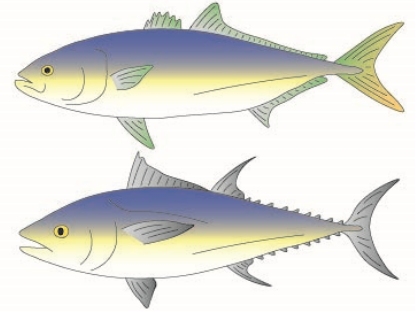
Myxozoa (multivalvulid species)



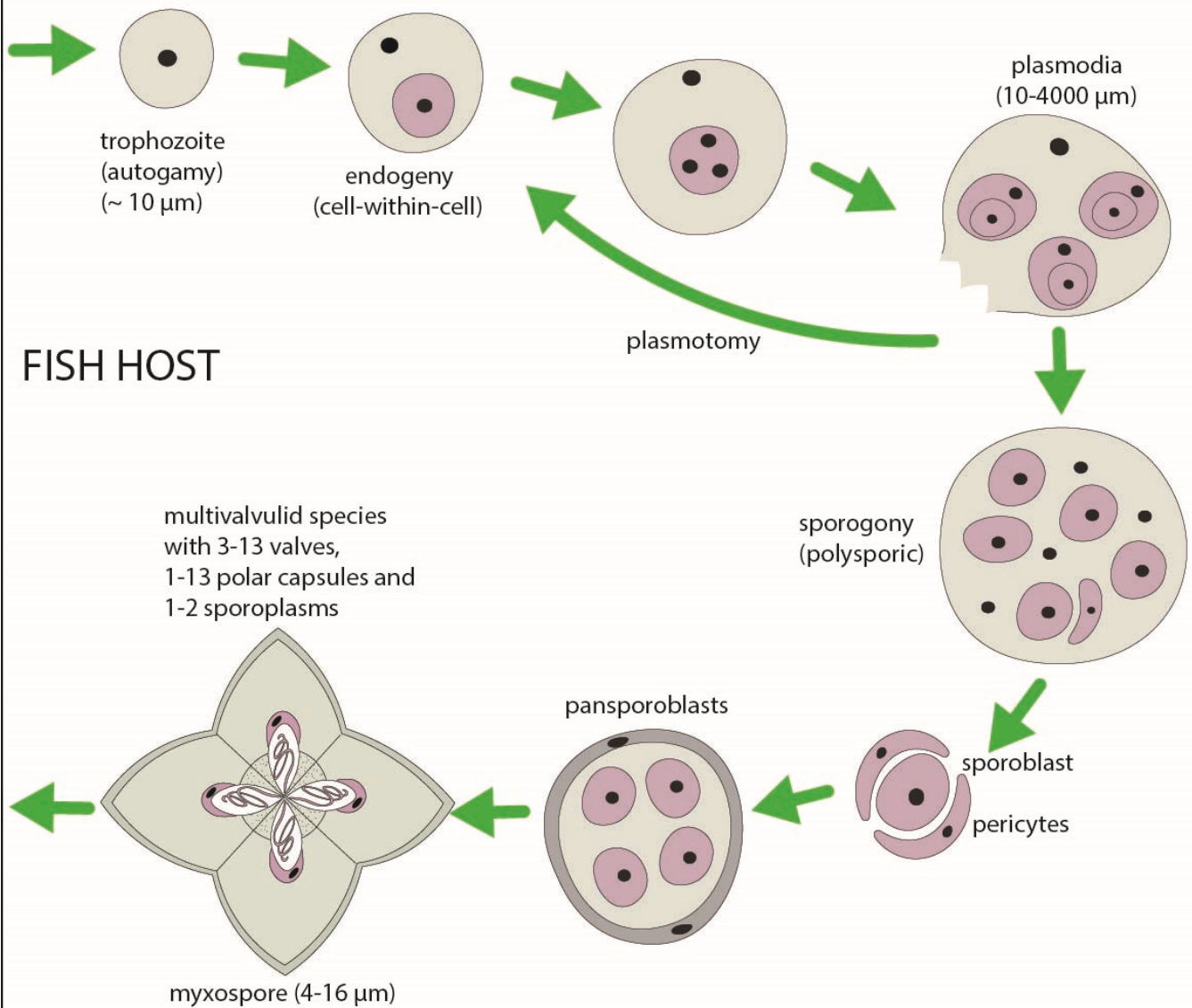
coelozoic/histozoic
(lesions/cysts, inflammation,
dysfunction, mortalities)

form unique multicellular spores
(with valvogenic, capsulogenic
and sporoplasmic cells)

discovered to have heteroxenous cycles
with myxospores developing in fish &
actinospores developing in worms



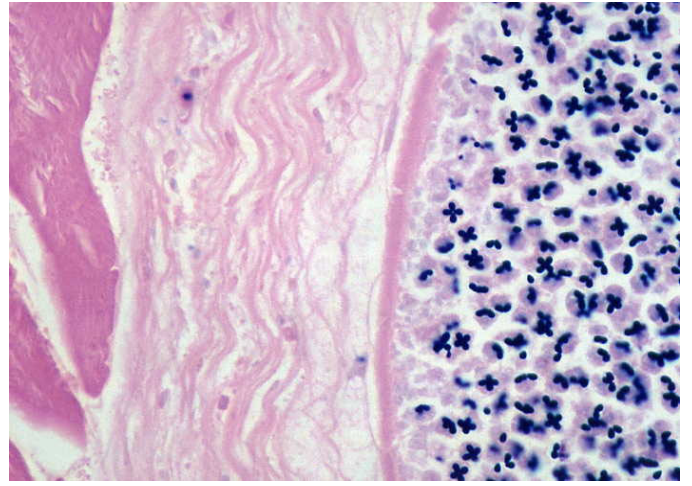
Vertebrate Hosts
(mainly marine fish)



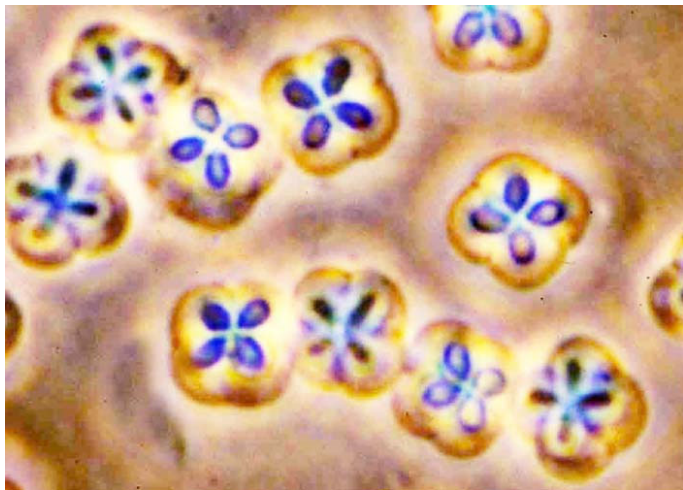
most life-cycles unknown, but studies have shown
myxospores to be infective to aquatic annelids
where they form actinospores infective to fish)
[actinospore cycle shown separately]



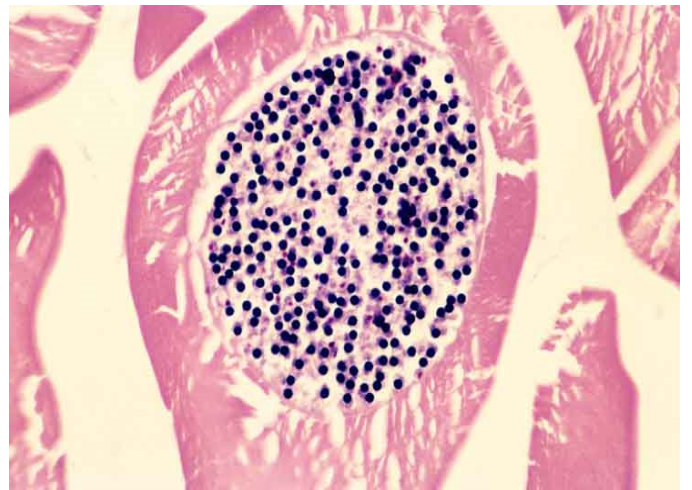
Kudoa cyst in fish muscle



Kudopa cyst wall in fish muscle



Kudoa spores from cyst in fish



Unicapsula cyst in fish muscle