Journal of Invertebrate Pathology 185 (2021) 107668

Contents lists available at ScienceDirect

Journal of Invertebrate Pathology

journal homepage: www.elsevier.com/locate/jip

A case report and statewide surveillance of "weak meat" condition of Alaska weathervane scallops, *Patinopecten caurinus*, linked to a recently identified pathogenic parasite, *Merocystis kathae* (Apicomplexa: Aggregatidae)

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ARTICLE INFO

Keywords:
Alaska weathervane scallops
Patinopecten caurinus
Parasite
Disease
Apicomplexan
Product Quality Issue

ABSTRACT

Weathervane scallop, *Patinopecten caurinus,* the largest scallop species in the world, is distributed from northern California, U.S.A., to the Bering Sea, and is only commercially harvested in Alaska. The fishery is considered well managed by the State of Alaska (U.S.A) Department of Fish and Game (ADF&G) and federal government, with many precautionary measures in place to avoid overharvest. There have been episodic declines in some management areas due to unknown causes. Fishermen also encounter scallops with abnormal adductor muscles, a condition colloquially termed "weak meat", characterized by the retention of muscle when shucked, an obvious darkened discoloration, and/or an abnormal texture making the product unacceptable for marketing. A similar syndrome in Atlantic sea scallops, *Placopecten magellanicus*, described as "gray meat", occurs in the eastern U.S. and Canada, and proposed causes include senescence, loss of bioenergetics due to chronic infestations, or a synergism of these factors. Recently a severe apicomplexan infection was found to cause a gray meat condition in Iceland scallops, *Chlamys islandica*, and the collapse of that stock. This parasite was subsequently detected in Atlantic sea scallops with the gray meat condition off the U.S. East Coast. Studies that followed identified the parasite as *Merocystis kathae*, previously described from the common whelk, *Buccinum undatum,* more than 100 years ago. In 2015 Bering Sea fishermen reported weak meat in their catch, so samples were submitted to ADF&G for diagnosis. Adductor muscles from all affected scallops had many large foci of an apicomplexan associated with necrosis, fibrosis, and muscular atrophy. Given the reduced quality, marketability, and possibly fitness of affected scallops, we performed a survey to estimate prevalence, intensity, and geographic distribution of this apicomplexan in Alaskan weathervane scallops. We sampled 180 scallops, from individual beds within each of the three major geographically broad scallop areas in Alaska. Overall prevalence was about 82%, ranging from 69 to 100% by district. Overall mean infection intensity, based on the number of parasite foci/section, was about 9 (range of 5–29, by location), with scallops from the Bering Sea and Southwest Kodiak being most severely infected. Molecular analyses confirmed that the Alaskan parasite is *M. kathae*, i.e., the same apicomplexan that caused the collapse of Icelandic scallops and a suspected cause for gray meat and mass mortality of Atlantic sea scallops in northeast North America.

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https://doi.org/10.1016/j.jip.2021.107668
Received 12 February 2021; Received in revised form 10 September 2021; Accepted 14 September 2021
Available online 20 September 2021

1. Introduction

Weathervane scallop, *Patinopecten caurinus*, the largest scallop species in the world, is distributed from northern California, U.S.A., to the Pribilof Islands in the Bering Sea, and is only commercially harvested in Alaska. The fishery first began in the 1960's due to the interests of scallop fisherman from the eastern U.S. that were faced with declining catches of Atlantic sea scallops, *Placopecten magellanicus*, on Georges Bank (Barnhart et al., 2008). Over-exploitation of the Alaskan fisheries occurred through the 1970's, which resulted in regulations adopting better management in the 1980's. The fishery has somewhat stabilized since then, however, though still with a slow and general downward trend in commercial landings since 2010 (North Pacific Fishery Management Council, 2011) caused by an array of known and unknown factors. The fishery is co-managed by the State of Alaska Department of Fish and Game (ADF&G) and the federal government under State and Federal fishery management plans with precautionary measures including a limited entry program, specific area and season catch quotas, gear and crew size restrictions, bycatch limits, an observer program, and area closures to minimize adverse benthic impacts (Kruse et al., 2005).

To date, the scallop fishery is considered well managed and sustainable. However, there have been episodes of declines in Catch Per Unit Effort (CPUE) in some management areas in the past. The cause(s) of these declines, under good management practices, are not fully known, but this has been investigated in some areas. In 2002, there was a dramatic decline in CPUE in the Cook Inlet Kamishak Bay District fishery and an unprecedented incidence of "clappers", i.e., dead scallops with valves connected but lacking soft tissues, found on the fishing grounds (Barnhart et al., 2008). Scallops were sampled from this 2002 fishery and analyzed by ADF&G's Fish Pathology Laboratory. High numbers of mud blisters consistent with *Polydora* infestation were noted to occur on the shells, the mantle tissue was reportedly atrophied, and the adductor muscle in a small percentage of the affected scallops had white foci. Six formalin-fixed scallops from this event were submitted to the Fish Pathology Laboratory for examination in early August 2002. Histopathology was performed and findings included 5/6 scallops having encysted spores of the gregarine *Nematopsis* sp. and 1/6 with an area of intense host inflammation that occasionally included abnormally enlarged cells with basophilic stippled nuclei and eosinophilic cytoplasm that were up to 2–3 times the size of normal host hemocytes. It was concluded that the condition was due to invasion of the shell by polychaete worms and associated tissue damage, abscess formation, and toxicosis from hydrogen sulfide due to the buildup of sediment, feces, and rejected material that becomes entrapped in the thick mucus secreted by the worms. The second case was submitted in mid-November 2002, from the Shelikof Strait District fishery, where again affected scallops were noted to have white foci distributed within the adductor muscle. One frozen scallop was submitted, histopathology was performed, and the only significant finding was occasional medium to small foci of host inflammatory hemocytes associated with necrosis of adductor muscle bundles and one small cytoplasmic inclusion containing apparent sporoplasms of an unidentified microsporidian-like organism. This case also involved *Polydora*-like mud blisters on the internal surface of the shell and a similar conclusion was made, but with the potential involvement of a second parasite that may have been a microsporidian. The submission of poor-quality frozen material of only one animal precluded a more rigorous examination and definitive interpretation, which frequently occurs with the opportunistic nature of these case submissions. Therefore, these examinations did not provide a conclusive explanation for the increased mortality in the stock but did suggest that it may have been linked to the reportedly high infestation by *Polydora* sp., a polychaete worm which burrows through the shell and causes toxic mortality (Barnhart et al., 2008).

More recently the abundance of scallops in some beds again showed signs of decline, which was observed in the 2013/14 Kodiak Shelikof District fishery. In response, managers aggressively reduced harvest quotas and began making in-season closures when fishery performance failed to maintain an adequate CPUE. In the following years, CPUE leveled off and began increasing in 2017/18 (North Pacific Fishery Management Council, 2019). The reason for this decline is currently unknown.

Fishermen and other industry stakeholders have frequently encountered scallops with abnormal adductor muscles, a condition that has been colloquially termed "weak meat". Weak weathervane scallop meats are characterized by the adductor muscle being retained on the viscera when shucked. The meat either tears apart and a portion of it remains attached to the viscera while the other portion remains attached to the top shell, or the meat remains whole, attached to the viscera, and detaches from the top shell. These meats may also be discolored (dark/grayish/brownish) or have a flaccid, stringy, or gelatinous texture that makes them unacceptable for marketing by the industry (Alaska Department of Fish and Game Shellfish Observer Program, 2019). Fishermen anecdotally report that the Yakutat registration area typically has some percentage of dark meats which fluctuates considerably each year. In contrast, dark meats are almost never found in the Kodiak registration area. Brenner et al. (2012) examined the quality of weak scallop meats using chemical and physical parameters and concluded that the values obtained from weak meat scallops were likely due to nutritional stress based on information in the published literature. A somewhat similar syndrome in Atlantic sea scallops, described as "gray meat", has been documented off the coast of the eastern U.S. and Canada. The first report was from the Bay of Fundy in 1936 and was suspected to be due to senescence (Stevenson, 1936). Medcof (1949) attributed this condition to increased energetic demands from chronic infestation by boring sponges (*Cliona* spp.). An intracellular prokaryote in the gills, plicate membranes, and other epithelial surfaces was associated with gray meat and mass mortality in the 1979/1980 season (Gulka et al., 1983). Similarly, Stokesbury et al. (2007) associated a mass mortality event involving gray meat in 2004–2005 with synergism of senescence and parasitism by shell borers and the intracellular prokaryote. More recently in Iceland a gray meat condition in Iceland scallops, *Chlamys islandica*, was found to be due to a severe apicomplexan infection that caused the collapse of that stock (Kristmundsson et al., 2015). This parasite was most closely related genetically to members of the apicomplexan genus *Aggregata* (Kristmundsson et al., 2015), which have a heteroxenous life cycle, with cephalopods as definitive hosts and crustaceans as intermediate hosts (Gestal et al., 2002). The apicomplexan identified in Iceland scallops was subsequently identified in the Atlantic sea scallops with gray meat in the eastern U.S., with confirmation by DNA sequencing (Inglis et al., 2016). Kristmundsson and Freeman (2018) then reported that the parasite was conspecific with *Merocystis kathae*, an apicomplexan previously described by Dakin (1911) from the common whelk, *Buccinum undatum,* more than 100 years ago. Foulon (1919) and Patten (1935) demonstrated that the whelk was the definitive host in its complex life cycle, while the intermediate host was unknown, but suggested it to be a crustacean. Furthermore, their results showed that *M. kathae* followed a seasonal developmental pattern. At present, pectinid scallops are known to serve as intermediate hosts (Kristmundsson and Freeman 2018).

The objective of this study was to investigate the presumptive role of infectious agents associated with the "weak meat" condition in weathervane scallops. A particular emphasis was made on the etiology and effect of apicomplexan infections based on a similar condition associated with high mortality in scallops in Icelandic waters and the "gray meat" phenomenon in scallops from Georges Bank, U.S.A., which both involve the apicomplexan species *M. kathae*. Molecular analyses were conducted to determine the relatedness of the Alaskan parasite to *M. kathae*.

2. Materials and methods

2.1. Diagnostic case study

In January 2015, the ADF&G Fish Pathology Laboratory received reports from the Kodiak field office of a weak meat condition in scallops caught in the Bering Sea. A case history was obtained, and a set of samples was submitted for diagnostic evaluation. Four affected scallops were formalin-fixed at sea and six apparently unaffected live scallops were also submitted for comparison.

2.1.1. Necropsy

A full necropsy was performed, including external and internal gross examination, as well as the evaluation of gill wet mounts and muscle squashes. Samples of adductor muscle, siphon, digestive gland, gills, labial palps, mantle, kidney, heart, and gonad were also fixed from these scallops in 10% seawater formalin for histopathological examination.

2.1.2. Histopathology

All formalin fixed material was processed for histological examination using standard techniques, i.e., embedded in paraffin, sectioned (6 μm) and stained with hematoxylin and eosin (HE).

2.2. Surveillance study

2.2.1. Sampling sites and sample collection

Adult weathervane scallops were collected from the commercial scallop fishery as an added research project with the Alaska Weathervane Scallop Observer Program from July to November 2015. There are three major regions of scallop beds in Alaska designated as Eastern, Central, and Western based on geographic location (Fig. 1). Sampling was designed to test 60 animals from each of the three major geographic regions. The 60 scallop samples were taken from multiple sub-areas to try to obtain representative locations within each region (Fig. 1). Although the distance across beds within each major geographic region can be quite large, it is likely that these beds are biologically connected (Mundy, 2005) . The exception would be beds of the Cook Inlet and Shelikof Strait area compared to those of East Kodiak (both within the Central region) because the Alaska Coastal Current splits between the Kenai Peninsula and Afognak Island. Additionally, the benthic habitats between these two bed locations differ in that the Cook Inlet and Shelikof Strait areas are muddy with poor water clarity whereas the East Kodiak beds are predominantly comprised of sand and gravel with much better water clarity. Scallops were caught from 37 to 146 m in depth. Gross field observations on muscle quality were only made on samples taken from Kamishak Bay. Shell height, sex, and percent of shell infestation by *Polydora* sp. were recorded at all sites. Adductor muscle samples were fixed in 10% seawater formalin at sea for histopathology. A small subsample of adductor muscle from each scallop was also fixed in 96% ethanol for potential molecular analysis.

2.2.2. Histopathology

All formalin fixed material was processed for histological examination using standard techniques, i.e., embedded in paraffin, sectioned (6 μm) and stained with hematoxylin and eosin (HE). The HE-stained sections were examined under a compound microscope and the number of apicomplexan parasite foci per tissue section were enumerated and used as an indicator for infection intensity. The size of these foci, which was driven by the numbers of individual parasite cells, was also noted. We assessed and described any host tissue responses.

2.2.3. Diagnostic PCR and SSU rDNA sequencing

For molecular examination, small pieces (approximately 20 mg) of ethanol-fixed adductor muscle from five selected scallops sampled in the surveillance study (one from Shelikof Kodiak; two from Bering Sea/Dutch Harbor; two from Southwest Kodiak) that were heavily infected based on histopathology were tested with the diagnostic PCR for the presence of the scallop apicomplexan, *Merocystis kathae*. Additionally, 12 other heavily infected samples from the surveillance study (eight from Yakutat; three from Bering Sea/Dutch Harbor; one from Shelikof Kodiak) as judged by histopathology were selected and used for extended sequencing of the small subunit ribosomal DNA (SSU rDNA) following the methods described by Kristmundsson and Freeman (2018). Only representative samples exhibiting obvious microscopic signs of disease and heavy apicomplexan infection were tested with the diagnostic PCR and sequenced for confirmation, as these analyses were not warranted on every sample that were diagnosed by histopathology. Lastly, tissue samples removed from histological blocks from 2002 were subjected to molecular analysis to confirm parasite presence. All the samples were placed into a lysis buffer for genomic DNA extraction using a GeneMATRIX kit (EURx Poland) following the tissue protocol provided in the kit (Cat. no. E3550). The apicomplexan SSU rDNA was amplified from the parasite using the diagnostic primers, 18e-Mer 5′ ctgccagtagttatacgt 3′ and Mer-790r 5′acacscttgaagcaccctac 3′, and PCR conditions as previously described by Kristmundsson et al., (2015). PCR bands of the expected size (772 bp) were recovered from the PCR

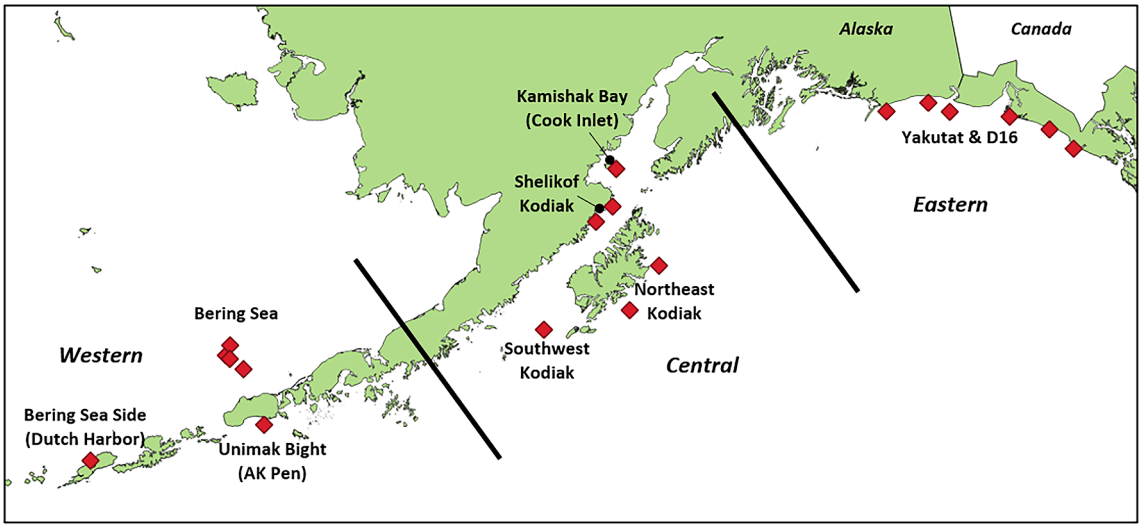

Fig. 1. Alaska scallop fishery management areas map showing locations (red diamonds) of samples taken for the surveillance study within each of the three major geographically broad scallop areas in Alaska (Eastern, Central and Western).

products using a GeneMATRIX PCR extraction kit (EURx Poland). All PCR reactions were performed in triplicate. Samples were also tested at a second laboratory in our group (that of SI and J. Koop) to assess reproducibility. Sequencing was conducted as previously described (Kristmundsson and Freeman, 2018) and reactions were performed using BigDyeTM Terminator Cycle Sequencing chemistry utilising the same oligonucleotide primers that were used for the original PCRs. DNA sequencing was performed in both forward and reverse directions for all PCR products and nucleotide BLAST searches were performed for each sequence to confirm an apicomplexan origin. The contiguous sequences were obtained manually using CLUSTAL_X and BioEdit (Hall, 1999).

2.3. Evaluation of archived material from historical cases

The discovery of an apicomplexan parasite in scallops with abnormal adductor muscles in Iceland, Faroe Islands, and eastern U.S.A. (Kristmundsson et al., 2011, 2015; Inglis et al., 2016) prompted investigation into two previous diagnostic cases involving weathervane scallops from 2002 (Barnhart et al., 2008). As mentioned earlier, the 2002 Kamishak Bay District fishery had dramatically reduced CPUE and an alarmingly high abundance of detected "clappers" found on the fishing grounds.

The histological slides were re-evaluated and 13 paraffin wax blocks from the two archived cases dating back to 2002 were dewaxed, and sectioned tissues were taken for DNA analysis. These represented tissues from four scallops; three from the August case that were the most infected as judged by histopathology and the single animal from the November case. PCR conditions were as described above (Section 2.2.3.), apart from increasing the cycles from 35 to 45. That was done to increase the sensitivity of the test, as formalin fixed tissues are not optimal for PCR.

3. Results

3.1. Diagnostic case study

3.1.1. Necropsy

The unaffected live scallops used as controls were active, with shells tightly closed when shucked. All six scallops had firm, white, adductor muscles. Gill wet mounts indicated a few *Licnophora*-like ciliates and various types of diatoms in two scallops. Four of the animals were females, two were males. There were no other remarkable findings at necropsy.

3.1.2. Histopathology

Histologic examination of the apparently unaffected live scallops that were submitted indicated that two scallops had low numbers of ciliated protozoa in the digestive tubules and intracellular prokaryote inclusions (3 and 15 colonies, respectively) in the gills. One scallop was infested with 5–6 *Licnophora*-like parasites in the siphon; one contained a single trichodinid-like parasite in a section of kidney; and one had low numbers of large, ciliated protozoa associated with heart tissue. Sections of labial palps from three scallops harbored a few ciliates. There was a 100% prevalence (6/6) of an apicomplexan parasite in the adductor muscle from the apparently normal scallops with a mean intensity of 1.5 parasite foci/section (range = 1–4) that was associated with necrosis, although areas of autolysis were also present. There were no remarkable findings in sections of mantle epithelium or gonad.

All four grossly affected scallops formalin-fixed at sea had an abundance of brown debris in the gills and a great deal of biofouling by barnacles and polychaetes presumed to be *Polydora* sp. The adductor muscle from these animals appeared to be torn, some with partial muscle still attached to the shell. The muscle was fragmented in several areas where fascicles became separated. There was a 100% prevalence (4/4) of an apicomplexan parasite in the adductor muscle from the grossly affected scallops with a mean intensity of 18 parasite foci/section (range = 12–23). One scallop had several white foci on the surface of the adductor muscle (Fig. 2a). Histological examination indicated one scallop had 3 colonies of an intracellular prokaryote in the gills and one with a focus of debris and bacteria in connective tissues of the mantle epithelium. Two scallops had a few gill ciliates. Adductor muscles from all four scallops had many (12–23) large foci of an apicomplexan

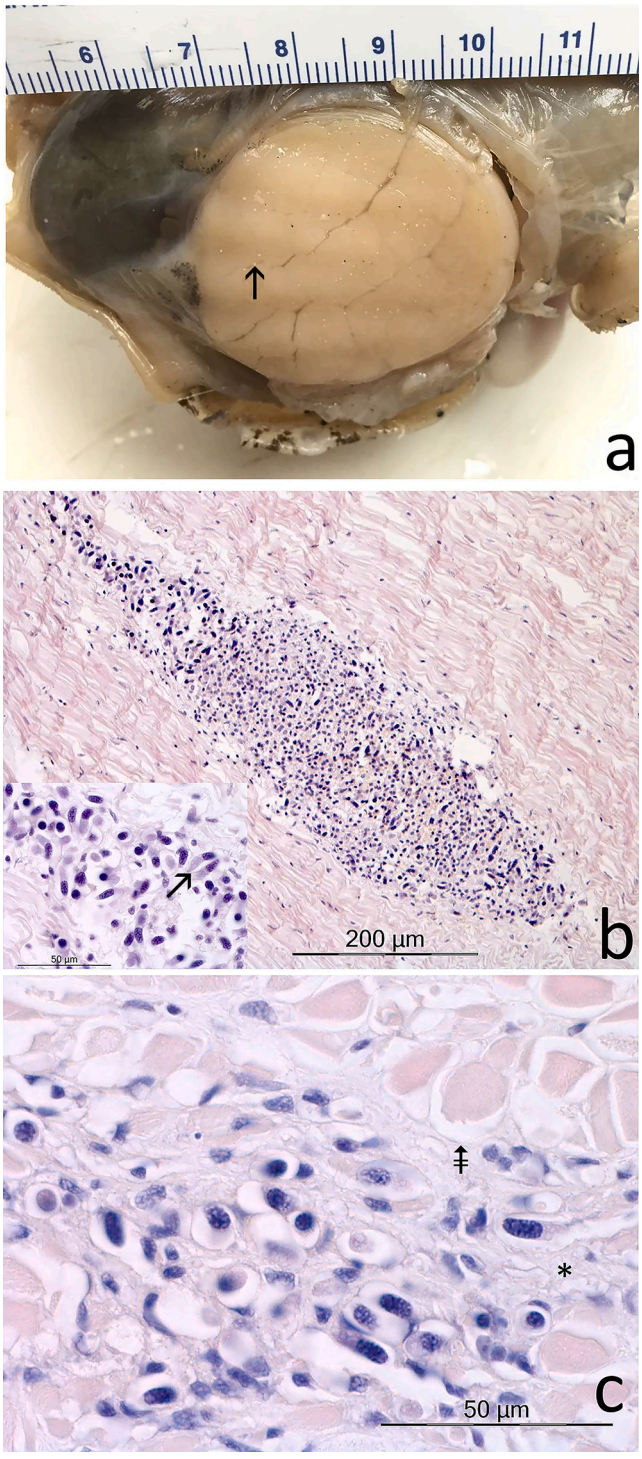

Fig. 2. Pathology of affected 'weak-meat' scallops from diagnostic case. (a) Grossly there were numerous small white foci throughout the adductor muscle; (b) Histologically the adductor muscle contained large basophilic foci of apicomplexan parasites within myocytes. Inset shows higher magnification of vermiform shaped parasites (arrow); (c) Necrosis (asterisk) was interspersed between the apicomplexan parasites and myocytes appeared atrophied (arrow with double hash marks).

parasite associated with necrosis and fibrosis, as well as muscular atrophy (Fig. 2b and c). There were no remarkable findings of sections from siphon, digestive tubules, kidney, labial palps, or gonad.

3.2. Surveillance study

3.2.1. Sampling sites and sample collection

Fig. 1 summarizes the sample collection locations of the study and Table 1 summarizes field data collected on *Polydora* infestation and mean shell height as well as apicomplexan prevalence and intensity derived from histopathology.

3.2.2. Histopathology

Table 1 summarizes the prevalence and intensity of apicomplexan infections by region. There was an overall prevalence of 82.2% (148/180), with a range among fishing districts from 68.3% to 100%. Overall mean intensity of infection based on the number of parasite foci/section was 9.3, with mean intensities ranging from 5.4 to 29.2 by sample location. Samples from the Bering Sea Side (Dutch Harbor) and Southwest Kodiak districts had the most severe infections; some sections contained more than 60 parasite foci. Parasite foci varied greatly in size, from 1 to 2 single intracellular organisms diffusely scattered to large distinct foci containing aggregates of 50–100+ organisms that obliterated the cell and displaced tissue. The latter were more associated with a chronic inflammatory response and granuloma-like formation (Fig. 3a). Myonecrosis (Fig. 3b) and fibrosis (Fig. 3c) were also observed. Several stages of the parasite were observed, including the common oval to vermiform shaped zoites with vacuolated cytoplasm and stippled nuclear chromatin (Fig. 3d), large immature meronts with a prominent nucleus and nucleolus (Fig. 3f), and large mature meronts lined with many curved merozoites forming a rosette-like convoluted network (Fig. 3e). All these stages represented those involved in the asexual reproduction phase of this parasite. Incidental findings included one sample with a metazoan parasite that resembled a nematode and one sample with a section of attached mantle that was infested with 17 individuals of an unidentified *Trichodina* sp.

Table 1
Summary of the prevalence and mean intensity of infection (parasite foci/section) of the apicomplexan parasite in the surveillance study by fishing district and overall. Field data on *Polydora* sp. infestation and mean shell height for each district are also presented. Parasite foci varied greatly in size, from 1 to 2 single intracellular organisms diffusely scattered to large distinct foci containing aggregates of 50–100 + organisms that obliterated the cell and displaced tissue.

District	Apicomplexan Prevalence (%) (positive/total)	Mean intensity of parasite foci (range)	*Polydora* prevalence (%) & mean intensity (% shell coverage)	Mean shell height, mm (range)
Northeast Kodiak	80 (16/20)	5.4 (1–16)	15 (11.7)	136.4 (100–155)
Shelikof Kodiak	100 (20/20)	10.2 (1–30)	5 (2)	141.1 (106–177)
Southwest Kodiak	90 (9/10)	22.6 (3–36)	20 (11.5)	153.8 (120–182)
Unimak Bight (AK Pen)	80 (8/10)	7.1 (1–16)	0	154.9 (127–173)
Bering Sea Side (Dutch Harbor)	100 (10/10)	29.2 (12–64)	0	163.6 (152–181)
Bering Sea	87.5 (35/40)	5.7 (1–14)	30 (4.5)	160.1 (121–181)
Yakutat & D16	68.3 (41/60)	6.8 (1–26)	51.7 (9.8)	124.5 (102–162)
Kamishak Bay (Cook Inlet)	90 (9/10)	6.2 (1–10)	100 (54.4)	158.4 (148–169)
Overall	82.2 (148/180)	9.3 (1–64)	32.8 (16.3)	142.9 (100–182)

3.2.3. Diagnostic PCR and SSU rDNA sequencing

The diagnostic PCR detected *M. kathae* DNA in all five selected scallops exhibiting clinical signs of weak meat. These results were also reproduced in the secondary laboratory. An additional 12 heavily infected samples were processed by the primary laboratory for sequencing of the SSU rDNA and the resulting nucleotide sequence was deposited to the GenBank database under accession number MN960514. All 12 samples were PCR-positive and 6 of the samples were selected and successfully sequenced (Table 2). The Alaskan isolate had a 99.8% match to the original *M. kathae* sequence isolated from Iceland scallops (GenBank Acc. No. MH348777).

3.3. Evaluation of archived material from historical cases

Re-examination of archived histological sections revealed the presence of an apicomplexan consistent with *M. kathae* within inflammatory foci of affected scallops. These were oval to vermiform shaped zoites with vacuolated cytoplasm and stippled nuclear chromatin (Fig. 4). There was also one example of larger mature meronts forming the early stages of the rosette-like convoluted network as seen in more recent cases (Fig. 4). Pathologic changes of infected scallop muscle in the 2002 cases also involved a chronic inflammatory response, granulomas, myonecrosis and fibrosis. Two samples from dewaxed paraffin blocks tested positive for *M. kathae* using the diagnostic PCR; these represented two separate animals (Table 2).

4. Discussion

Based on histopathology and SSU rDNA sequencing, we conclude that the apicomplexan parasite infecting Alaska weathervane scallops is *M. kathae*. This parasite has also been found in Atlantic sea scallops on the East coast of USA (Inglis et al., 2016), Iceland scallops in Iceland, and king and queen scallops in Scottish and Faroese waters (Kristmundsson et al., 2011; Soares et al., 2021). It had a 99.8% SSU rDNA sequence identity to *M. kathae*. The sequence of the Alaskan isolate only differed by two nucleotides from those obtained from Atlantic sea scallops and Iceland scallops, which were located near the end of the sequence and may represent sequencing errors from the original sequence from Iceland (GenBank Acc. No. MH348777). Additionally, we conclude that this parasite is likely linked to the poor quality of infected adductor muscle in these scallops as the infection represents a space occupying lesion and can elicit severe host tissue changes. Adductor muscle is a vital energy resource for scallops, particularly during gametogenesis (Cragg, 2016; Robinson et al., 1981) and Inglis et al. (2016) showed that gray meat scallops that were more heavily infected with this parasite had significantly less carbohydrate and protein content as well as increased moisture compared to normal scallops, thus affecting scallop condition. There have not been any other infectious agents detected in affected tissues that appear capable of causing this condition. Given the physiological impacts on individual hosts, it is plausible that this parasite has the potential to cause population level impacts. Indeed, Kristmundsson et al. (2015) and Kristmundsson and Freeman (2018) have proposed that this parasite is largely responsible for mass mortalities in Iceland and possibly also elsewhere in the Northern Hemisphere. Even scallops with low intensity infections (i.e., subclinical) may display clinical signs when subjected to other stressors, such as spawning or poor nutrition, which may represent important co-factors for increasing parasite load or reducing infection resilience to the point of disease manifestation (Inglis et al., 2018). However, scallops with overt disease due to high infection intensities unrelated to predisposing abiotic or biotic stressors may also occur through stochastic effects where some just have higher infections due to the randomness of exposure. Recently Siemann et al (2019) proposed that the cause of gray meats in Atlantic

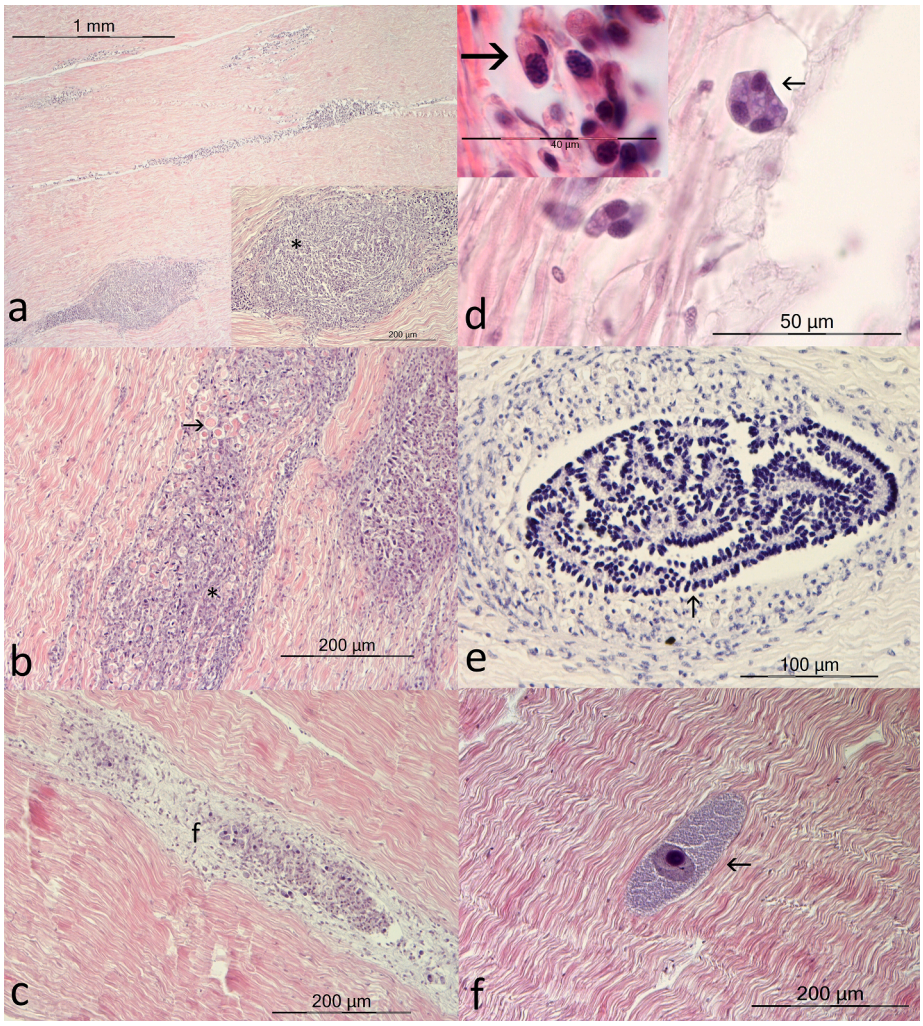

Fig. 3. Histopathology of 'weak-meat' scallops from surveillance study showing a massive, disseminated apicomplexan infection in scallop adductor muscle. (a) Several large foci containing many parasites. Inset shows a chronic inflammatory response that resembles a granuloma (asterisk); (b) Severe myositis (asterisk) and myonecrosis (arrow) associated with the presence of apicomplexan zoites; (c) Fibrosis (f); (d) Scallop adductor muscle showing clusters of several vermiform shaped apicomplexan parasites with vacuolated cytoplasm and stippled nuclear chromatin (arrow). Inset shows a zoite within a host cell (arrow); (e) A mature meront stage of the apicomplexan parasite comprised of numerous curved merozoites (arrow) forming a rosette-like convoluted network associated with a chronic inflammatory response; (f) Scallop adductor muscle showing an immature meront stage (arrow) of the apicomplexan parasite with a prominent nucleus and nucleolus.

Table 2
Summary of the molecular testing performed on different material in this study. Sample size and results from the diagnostic PCR (Kristmundsson et al., 2015) and Small Subunit ribosomal DNA (SSU rDNA) sequencing (Kristmundsson and Freeman 2018) are presented. No molecular analyses were performed in the initial diagnostic case. These tests were not performed on samples from the initial diagnostic case as the cause of morbidity was unknown at sample submission so only a standard necropsy and histopathology were used in this initial screening. Two sets of samples from the surveillance study were tested, with six samples sequenced (#'s 31, 35, 97, 141, 147, and 149). * = 13 paraffin wax blocks from two archived cases representing tissues from four scallops: three most heavily infected samples (by histology) from the August case and single animal from November case. ** = PCR-positive results were from two animals (#s 4 and 6). ND = Not Determined.

Study Type	Sample size	Diagnostic PCR	SSU rDNA sequencing
Surveillance study	17 (5; 12)	5/5; 12/12	ND; 6/12
Archived material*	13	2/13**	ND

sea scallops is not driven by this pathogenic parasite based on modeling of abiotic and biotic factors, finding that location and reproductive stage correlated, but they excluded disease assessment. Furthermore, they contended that the cause is multifactorial and placed more emphasis on factors other than disease caused by this pathogen. The severe histopathologic changes in heavily infected scallops are most likely responsible for most of the noticeably poor gray meats, which may be exacerbated or precipitated by environmental factors and host physiology. However, this is a normal paradigm in disease ecology, and it is improbable that the high degree of severe gray meats would occur in the absence of this pathogen.

As previously stated, earlier studies in eastern Canada and the U.S. attributed population crashes in Atlantic sea scallops to either senescence (Stevenson, 1936), infections of the gill (Gulka et al., 1983) and shell (Medcof, 1949), or synergism of senescence and parasitism (Stokesbury et al., 2007). However, the infections in those studies did not involve adductor muscle tissue and thus the connection is more tenuous than for the pathogenic apicomplexan in our study. Likewise, Brenner et al. (2012) concluded that the poor quality of weathervane scallop meats in the Alaska fishery may have been due to nutritional stress. In 2016, the apicomplexan, later identified as *M. kathae*, was identified in adductor muscles of Atlantic sea scallops exhibiting gray meat condition (Inglis et al 2016) and subsequently in the definitive host, the common whelk, *B. undatum*, from Georges Bank (Inglis et al., 2018). The tissue responses and space occupying lesions within the adductor muscle of scallops caused by *M. kathae* supports the conclusion that this parasite is most likely responsible for the weak meat condition and possibly mass mortalities that could account for the poor recovery of this fishery despite best management practices. Indeed, the scallop adductor muscle functions both for shell closure and locomotion to avoid predators, so a weakened adductor caused by infection results in a compromised animal that is less equipped to survive in the environment and are at an increased risk for predation, such as from whelks, the only known definitive hosts of *M. kathae* (Kristmundsson and Freeman, 2018). Although the definitive host of *M. kathae* is still unknown in Alaskan

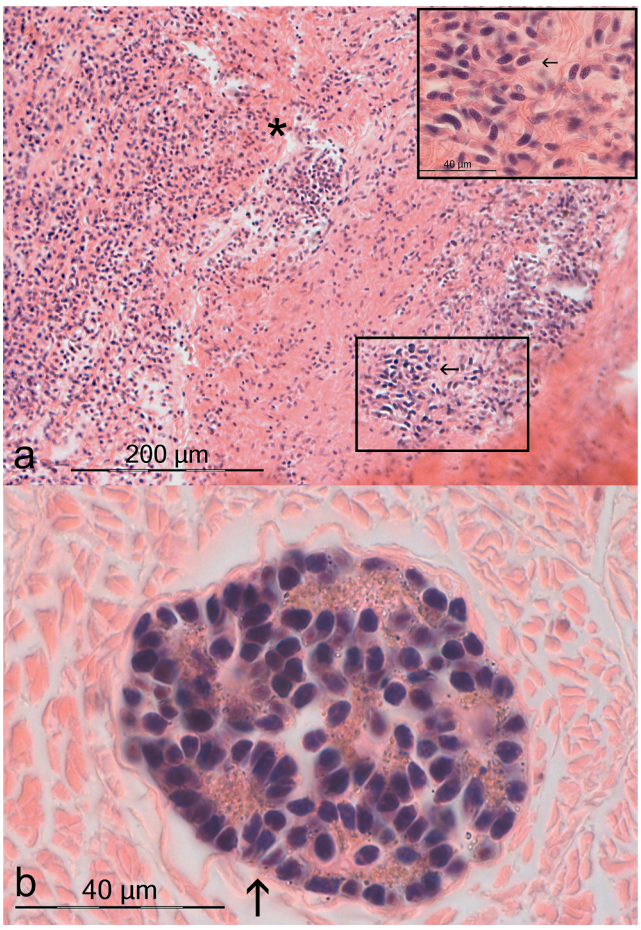

Fig. 4. Histopathology of 'weak-meat' scallops from 2002 archived cases. (a) Massive, disseminated apicomplexan (arrow) infection in scallop adductor muscle associated with severe myositis (asterisk). Inset shows higher magnification of several oval to vermiform shaped zoites (arrow) with vacuolated cytoplasm and stippled nuclear chromatin that were identical to *Merocystis kathae* from recent cases; (b) A mature meront stage of the apicomplexan parasite comprised of numerous straight or curved merozoites (arrow) forming an early rosette-like convoluted network.

waters, it is most likely a buccinid gastropod, based on previous research (Kristmundsson and Freeman, 2018). Therefore, in terms of Alaskan waters, predation/scavenging of native whelks on moribund/dead weathervane scallops would further sustain the life cycle of the parasite, consequently increasing the infectious load in the ecosystem.

Determining the cause(s) of population declines of wild organisms is challenging and complex for multiple reasons, such as a lack of standardized protocols for mortality investigations, a limited scope of analyses performed, and an absence of a centralized database for tracking mortality events. Furthermore, the most impacted animals quickly die or are removed from the ecosystem by predators (La and Cooke, 2011). Such investigations rarely incorporate infectious diseases as a factor and if infections are studied, then prevalence alone is typically reported. However, prevalence yields a weak assessment of macroparasite impacts (Dobson and Hudson, 1986) because these parasites typically have an aggregated distribution within the host population, with most hosts harboring few or no parasites (Galvani, 2003). Therefore only a few animals within the population may be heavily infected, and these may die prior to sampling. Although apicomplexans may be regarded as microparasites due to their small size, some species also have features of macroparasites, such as complex life cycles. Anderson and May (1979) defined microparasites as organisms that reproduce directly in the invaded individual host, usually inducing long lasting immunity to reinfection and typically causing transient infections (e.g., bacteria and viruses). In contrast, macroparasites do not multiply within a host (the load is thus determined by invasion events), generally elicit a short-term immune response and induce chronic infections associated with a longer life expectancy of the parasite (e.g., helminths). Some parasites may have features of both models. For example, Ferguson et al. (2011) showed that myxozoan parasites, which are small metazoans related to cnidarians, display features of microparasites in that asexual reproduction occurs in the fish host. However, they also resemble macroparasites in that plasmodial pseudocysts, which grow due to the proliferation of a single progenitor cell, do not increase in number within the host and infections persist throughout the juvenile life stages of the fish host (Ferguson et al., 2010). Therefore, apicomplexans with complex life cycles, like the one in this study, may represent a mixed model with features of both systems.

Despite the limitations of evaluating the role of parasitism in host population declines, there have been some methodologies devised to estimate the effects, which differ by the type of parasitism. Lester (1984) provided a summary review of methods for estimating parasite-associated mortality in wild fishes. These included: 1) through necropsy and diagnostic testing of affected fish; 2) performing infection challenges with naïve fish under controlled laboratory conditions; 3) observing a decrease in prevalence of a long-lived parasite with host age; 4) observing a decrease in the variance/mean ratio for parasites with host age; 5) comparing the observed frequency of a combination of two independent events with the calculated probability of their occurrence; and 6) comparing the observed frequency distribution of the parasite with a predicted distribution based on data from lightly-infected fish. Although each of these methods have their own unique limitations, they are essentially the only tools available to estimate parasite-associated mortality in wild organisms. Our study utilized the first method of performing a diagnostic evaluation on affected scallops and the results indicated that *M. kathae* is associated with gross and histopathologic lesions consistent with disease of individual scallops that could cascade up to population level impacts for these hosts. Indeed, Kristmundsson et al. (2015) have shown that this parasite is strongly linked to the collapse of Iceland scallops and subsequently Kristmundsson and Freeman (2018) have reported on mass mortalities associated with *M. kathae* in numerous commercial scallop populations throughout the Northern Hemisphere.

The circumpolar distribution of this parasite is fascinating considering that both the scallop and whelk hosts do not migrate long distances and thus a mechanism for dispersal is not straightforward. Although speculative, perhaps it was introduced via ballast water from scallop fishing vessels that moved from the eastern U.S. seaboard to Alaska during the 1960's due to the closure of the scallop fishery on the East Coast of North America. The converse could also be plausible where it was transported from Alaska to the Atlantic via ballast water from ships returning from the Alaskan fishery. Given the earlier reports of gray meat scallops in the Bay of Fundy (Canada) in the 1930's, the most logical directionality of a presumed industry-associated transfer of this parasite would be from the Atlantic to the Pacific Ocean. Of course, the parasite may have been established in these hosts for millions of years prior to the ice ages that created more rigid physical barriers. That would assume that there was some mixing of larval drift zones, particularly in the Arctic Ocean, that would allow for parasite transmission between hosts. Indeed, there are some published data indicating that there may be a continuous distribution of scallop species in the Arctic Ocean and into the Bering Strait. The Iceland scallop (*C. islandica*) is found along East and West Greenland, around Iceland, along the Norwegian coast, northwestern Spitzbergen, around Svalbard, and in the White Sea, Kara Sea, and the Murman Coast of northeastern Russia (Ockelmann, 1958; Wiborg, 1963; Lubinsky, 1980; Hansen and Nedreaas, 1986; Sundet and Fevolden, 1994). The Iceland scallop has also been recorded from the Bering Strait and surrounding Pacific Ocean, the Okhotsk Sea, and down the eastern Pacific Coast as far South

as Puget Sound (Mottet, 1979). However, Waller (1991) considers *C. islandica* as limited to the sub-arctic regions of the North Atlantic and that records from the North Pacific are due to taxonomic confusion with closely related species. Regardless of the initial source, the discovery of this pathogenic parasite and its associated impacts on host physiology and survival has been invaluable information for resource managers tasked with evaluating these populations for harvest.

Unfortunately, there is little that can be done to mitigate this disease in a wild population of scallops. Kristmundsson and Freeman (2018) suggested that a targeted removal of whelks, the definitive host for *M. kathae*, from valuable scallop grounds would be advantageous to minimize the occurrence of *M. kathae* epizootics and prevent damaging economic losses. However, as the only known definitive host for this apicomplexan, *Buccinum undatum*, is absent from Alaskan waters, the gastropod host for *M. kathae* is unknown in the territory of the weathervane scallop. Furthermore, Inglis et al. (2017) has shown that the infection can be transmitted to naïve scallops from those previously infected when cohabitated or in bath exposures containing infected scallop tissues. However, there was no transmission of the parasite between infected live scallops, suggesting that the direct transmission of infection in nature occurs only when infected scallops die, and the decaying tissue releases infectious zoites to nearby scallops where they are ingested through filter feeding. Therefore, the practice of discarding offal at sea may be counterproductive. Direct transmission between intermediate hosts is a rare life cycle strategy for apicomplexans. The best-known example is that of *Toxoplasma gondii* where genetic testing indicated that recent strains have evolved to be capable of direct oral transmission between intermediate hosts (Su et al., 2003). Ceasing the practice of discarding scallop offal at sea may help reduce infections within the population, but this is impractical due to the huge monetary cost to fisherman. Pilot studies have indicated that a freshwater rinse of the offal prior to discard may be efficacious at reducing parasite transmission, presumably by reducing the parasitic load of extracellular zoites that become rinsed out of the tissues (Inglis, pers. comm.). Additional studies could be performed to determine a practical solution for decreasing the spread of infection from industry practices now that the discovery of this parasite and its impacts on scallop hosts have been determined.

In conclusion, we identified the apicomplexan parasite infecting weak meat-affected weathervane scallops as *M. kathae*. This parasite has also been found in king and queen scallops (Kristmundsson et al., 2011; Soares et al., 2021). It had a 99.8% SSU rDNA sequence identity to *M. kathae*. *Merocystis kathae* has been shown to be a pathogenic species in several pectinid hosts where it causes gross and microscopic tissue changes and mass mortality across the Northern Hemisphere. We also showed that archived material can be used to reassess diagnoses by using the more sophisticated molecular technologies available today. We re-evaluated case material from moribund scallops collected in the collapsing 2002 Kamishak Bay fishery and found that this parasite was associated with histopathology consistent with a weak meat type syndrome that most likely contributed to that event. Furthermore, we were able to confirm the presence of *M. kathae* DNA in these archived samples by PCR. This was somewhat surprising due to poor quality DNA in archived tissues that were originally fixed in Bouin's solution, which is extremely acidic with a pH of < 1. Future work will focus on the life cycle, specifically determining the definitive host species off the coast of Alaska because the common whelk does not occur in this region. It is likely to involve a closely related species (or multiple) that belong to the family Buccinidae as most apicomplexans display a high degree of host-specificity for the definitive host (Votýpka et al., 2016). There are over 20 buccinid species that occur in Alaska, with *Buccinum* and *Neptunea* being the most common genera and certain species have a circumpolar distribution, such as *Buccinum scalariforme* (Foster, 1979). Elucidating the life cycle of this highly pathogenic apicomplexan that causes large impacts on the scallop host will be hugely beneficial to the industry and resource managers that previously lacked knowledge about this limiting factor for scallop populations.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank ADF&G staff Ian Dickson for histotechnical assistance, Miranda Westphal for technical assistance in planning the surveillance study design, and staff of the Alaska Weathervane Scallop Observer Program for assistance with obtaining samples. The work by ADF&G Fish Pathology Laboratory staff was supported with funds through the Commercial Fisheries and Sport Fish Divisions of the Alaska Department of Fish and Game. This is contribution PP-CFPP-291 of the Alaska Department of Fish and Game, Division of Commercial Fisheries.

References

Alaska Department of Fish and Game Shellfish Observer Program (ADF&G), 2019. Scallop Observer Training and Deployment Manual. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak, Alaska.

Anderson, R.M., May, R.M., 1979. Population biology of infectious diseases: Part I. Nature. 280, 361–367. https://doi.org/10.1038/280361a0.

Barnhart, J.P., Sagalkin, N.H., Rosenkranz, G.E., Berceli, R.S., Stratman, J.P., Trowbridge, C.E., 2008. Annual Management Report for the commercial weathervane scallop fisheries in Alaska, 2005/06. Alaska Department of Fish and Game, Fishery Management Report No. 08-01, Anchorage, Alaska.

Brenner, K., Oliveria, A., Rosenkranz, G., Burt, R., Spafard, M., Bechtel, P.J., Crapo, C.A., Ralonde, R., 2012. Quality of weathervane scallops (*Patinopecten caurinus*) From Eastern and Western Gulf of Alaska. J. Shellf. Res. 31, 1123–1132. https://doi.org/10.2983/035.031.0423.

Cragg, S.M., 2016. Biology and Ecology of Scallop Larvae. In: Shumway, S.E., Parsons, G. J. (Eds.), Scallops: Biology, Ecology, Aquaculture, and Fisheries. Elsevier, Amsterdam, Netherlands, pp. 31–83.

Dakin, W.J., 1911. Notes on a new coccidian (*Merocystis kathae* n. gen. et sp.), occurring in the renal organ of the whelk. Arch. Protistenkunde Jena 23 (145–153), 119.

Dobson, A.P., Hudson, P.J., 1986. Parasites, disease and the structure of ecological communities. Trends Ecol. Evol. 1, 11–15. https://doi.org/10.1016/0169-5347(86)90060-1.

Ferguson, J.A., Koketsu, W., Ninomiya, I., Rossignol, P.A., Jacobson, K.C., Kent, M.L., 2011. Mortality of coho salmon (*Oncorhynchus kisutch*) associated with burdens of multiple parasite species. Int. J. Parasitol. 41, 1197–1205. https://doi.org/10.1016/j.ijpara.2011.07.005.

Ferguson, J.A., Schreck, C.B., Chitwood, R., Kent, M.L., 2010. Persistence of infection by metacercariae of *Apophallus* sp., Neascus sp., and *Nanophyetus salmincola* plus two myxozoans (*Myxobolus insidiosus* and *Myxobolus fryeri*) in coho salmon *Oncorhynchus kisutch*. J. Parasitol. 96, 340–347. https://doi.org/10.1645/ge-2289.1.

Foulon, C., 1919. *Merocystis Kathae* Dakin une aggregate de *Buccinum undatum*. Cellule. 30, 121–149.

Foster, N.R., 1979. A synopsis of the marine prosobranch gastropod and bivalve mollusks in Alaskan waters (M.S, thesis). University of Alaska, Institute of Marine Science, Fairbanks, Alaska, p. 807 pp..

Galvani, A.P., 2003. Immunity, antigenic heterogeneity, and aggregation of helminth parasites. J. Parasitol. 89, 232–241. https://doi.org/10.1645/0022-3395(2003)089[0232:IAHAAO]2.0.CO;2.

Gestal, C., Guerra, A., Pascual, S., Azevedo, C., 2002. On the life cycle of *Aggregata eberthi* and observations on *Aggregata octopiana* (Apicomplexa, Aggregatidae) from Galicia (NE Atlantic). Europ. J. Protistol. 37, 427–435. https://doi.org/10.1078/0932-4739-00817.

Gulka, G., Change, P.W., Marti, K.A., 1983. Prokaryotic infection associated with a mass mortality of the sea scallop. *Placopecten magellanicus*. J. Fish Dis. 6, 355–364. https://doi.org/10.1111/j.1365-2761.1983.tb00087.x.

Hall, T.A., 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symp. Series 41, 95–98. https://doi.org/10.14601/Phytopathol_Mediterr-14998u1.29.

Hansen, K., Nedreaas, K., 1986. Measurements of Iceland scallop (Chlamys islandica Müller) in the Spitzbergen and Bear Island regions. International Council for the Exploration of the Sea CM 1968/K:26. 19p.

Inglis, S., Kristmundsson, Á., Freeman, M.A., Levesque, M., Stokesbury, K., 2016. Gray meat in the Atlantic sea scallop, *Placopecten magellanicus*, and the identification of a known pathogenic scallop apicomplexan. J. Invertebr. Pathol. 141, 66–75. https://doi.org/10.1016/j.jip.2016.10.008.

Inglis, S.D., Georgianna, D., Kristmundsson, Á., Freeman, M.A., Koop, J., 2017. At sea discard of gray meat tissue as a vector for apicomplexan transmission in Atlantic sea scallop Placopecten magellanicus. International Pectinid Workshop. April 19-25, 2017. Portland, Maine.

Inglis, S.D., Koop, J., Kristmundsson, Á., Freeman, M.A., Georgianna, D., 2018. Transmission of apicomplexan infection in gray meat Atlantic sea scallops. National Shellfisheries Association's 110th Annual Conference. March 2018. Seattle, Washington.

Kristmundsson, Á., Erlingsdóttir, Á., Freeman, M.A., 2015. Is an apicomplexan parasite responsible for the collapse of the Iceland scallop (*Chlamys islandica*) Stock? PLoS ONE 10 (12), e0144685. https://doi.org/10.1371/journal.pone.0144685.

Kristmundsson, Á., Freeman, M., 2018. Harmless sea snail parasite causes mass mortalities in numerous commercial scallop populations in the northern hemisphere. Scientific Reports. 8, 7865. https://doi.org/10.1038/s41598-018-26158-1.

Kristmundsson, Á., Helgason, S., Bambir, S.H., Eydal, M., Freeman, M., 2011. Previously unknown apicomplexan species infecting Iceland scallop, *Chlamys islandica* (Müller, 1776), queen scallop, *Aequipecten opercularis* L., and king scallop. *Pecten maximus* L. J. Invertebr. Pathol. 108, 147–155. https://doi.org/10.1016/j.jip.2011.08.003.

Kruse, G.H., Barnhart, J.P., Rosenkranz, T.E., 2005. Management of the data-limited weathervane scallop fishery in Alaska. In: Kruse, G.H., Gallucci, V.F., Hay, D.E., Perry, R.I., Peterman, R.M., Shirley, T.C., Spencer, P.D., Wilson, B., Woodby, D. (Eds.), Fisheries assessment and management in data-limited situations. Alaska Sea Grant College Program, Fairbanks, Alaska, pp. 51–68.

La, V.T., Cooke, S.J., 2011. Advancing the science and practice of fish kill investigations. Rev. Fish. Sci. 19, 21–33. https://doi.org/10.1080/10641262.2010.531793.

Lester, R., 1984. A review of methods for estimating mortality due to parasites in wild fish populations. Helgol. Mar. Res. 37, 53–64. https://doi.org/10.1007/BF01989295.

Lubinsky, L., 1980. Marine bivalve molluscs of the Canadian central and eastern Arctic: faunal composition and zoogeography. Can. Bull. Fish. Aquat. Sci. 207, 1–111.

Medcof, J.C., 1949. Dark-meat and the shell disease of scallops. Prog. Rep. Atlantic Coast Stations 45, 3–6.

Mottet, M.G., 1979. A review of the fishery biology and culture of scallops. State of Washington Department of Fisheries, Technical. Report. 39, 292p.

Mundy, P.R., 2005. The Gulf of Alaska: Biology and Oceanography. Alaska Sea Grant College Program. University of Alaska Fairbanks. https://doi.org/10.4027/gabo.2005.

North Pacific Fishery Management Council, 2011. Stock Assessment and Fishery Evaluation Report for the Scallop Fishery off Alaska. North Pacific Fishery Management Council, 605 West, 4th Avenue,. Suite 306, Anchorage, Alaska.

North Pacific Fishery Management Council, 2019. Stock Assessment and Fishery Evaluation Report for the Scallop Fishery off Alaska. North Pacific Fishery Management Council, 605 West, 4th Avenue,. Suite 306, Anchorage, Alaska.

Ockelmann, W.K., 1958. The zoology of East Greenland. 4. Marine Lamellibranchiata. Medd. Grønl. Kom. Ledel. Geol. Geogr. Unders. Grønl. 122, 1–256.

Patten, R., 1935. The life history of *Merocystis kathae* in the whelk, *Buccinum undatum*. Parasitol. 27, 399–430. https://doi.org/10.1017/S0031182000015328.

Robinson, W.E., Wehling, W.E., Morse, M.P., McLeod, G.C., 1981. Seasonal changes in soft-body component indices and energy reserves in the Atlantic deep-sea scallop, *Placopecten magellanicus*. Fish. Bull. 79, 449–458.

Siemann, L.A., Garcia, L.M., Huntsberger, C.J., Smolowitz, R.J., 2019. Investigating the impacts of multiple factors on gray meats in Atlantic sea scallops (*Placopecten magellanicus*). J. Shellf. Res. 38, 233–243. https://doi.org/10.2983/035.038.0203.

Soares, S.M.C., Blackadder, L., Stagg, H.E.B., Munro, E.S., McLay, A., 2021. The presence of Apicomplexan parasites in king scallops (*Pecten maximus*) in Scottish waters. J. Invertebr. Pathol. 178, 107508 https://doi.org/10.1016/j.jip.2020.107508.

Stevenson, J.A., 1936. The Canadian Scallop: its Fishery, life-History and Some Environmental Relationships (MS thesis). University of Western Ontario, p. 201 pp..

Stokesbury, K.D.E., Harris, B.P., Marino II, M.C., Nogueira, J.I., 2007. Sea scallop mass mortality in a marine protected area. Mar. Ecol. Prog. Ser. 349, 151–158. https://doi.org/10.3354/meps07113.

Su, C., Evans, D., Cole, R.H., Kissinger, J.C., Ajioka, J.W., Sibley, L.D., 2003. Recent expansion of *Toxoplasma* through enhanced oral transmission. Science. 299, 414–416. https://doi.org/10.1126/science.1078035.

Sundet, J.H., Fevolden, S.E., 1994. Distribution of the Icelandic scallop, Chlamys islandica, in the northeast Atlantic. In: Bourne, N.F., Bunting, B.L., Townsend, L.D. (Eds.), Proceedings of the 9th International Pectinid Workshop, Nanaimo, B.C., Canada, April 22-27, 1993. Can. Tech. Rep. Fish. Aquat. Sci. 2, 179.

Votýpka, J., Modrý, D., Oborník, M., Šlapeta, J., Lukeš, J., 2016. Apicomplexa. In: Archibald, J. (Ed.), Handbook of the Protists. Springer, Cham. https://doi.org/10.1007/978-3-319-32669-6_20-1.

Waller, T.R., 1991. Evolutionary relationships among commercial scallops (Mollusca: Bivalvia: Pectinidae). In: Shumway, S.E. (Ed.), Scallops: Biology, Ecology, and Aquaculture. Elsevier Press, pp. 1–73.

Wiborg, K.F., 1963. Some observations on the Iceland scallop *Chlamys islandica* (Müller) in Norwegian waters. Fiskeridirektoratets Skrifter Serie Havundersøkelser (Rep. Norweg. Fish. Mar. Invest.) 13, 38–53.