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1 **A review of the characteristics of the dinoflagellate parasite *Ichthyodinium***  
2 ***chabelardi* and its potential effect on fin fish populations**

3

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18

19 Key words: Osteichthyes; Syndiniophyceae; *Amyloodinium ocellatum*; *Saprolegnia*

20 *parasitica*; *Sphaerothecum destruens*; X-cell species

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23

24 Abstract

25

26 This paper focuses on the biology and ecological impacts of *Ichthyodinium chabelardi*  
27 (Phylum Dinophyta, Class Syndiniophyceae, Order Syndiniales), a virulent endobiotic  
28 parasite of yolk sacs and young larvae of many species of marine fin fish. Its infections  
29 have been observed in warm and temperate open oceanic environments and crowded  
30 marine fish tanks. The prevalence of *I. chabelardi* and the range of its host fishes is not  
31 well-studied, and our understanding of its life cycle is incomplete. Here we describe what  
32 is known about *I. chabelardi* infections in fish and we compare this with several other  
33 protistan parasites of fish, including *Amyloodium ocellatum*, *Saprolegnia parasitica*,  
34 *Sphaerothecum destruens*, and the “X-cell” clades *Gadixcellia* and *Xcellia*, all of which  
35 are considered emerging generalist parasites infecting a wide variety of fin fish species.  
36 Recent findings suggest that rising seawater temperatures might lead to higher infection  
37 rates in fishes, and we expect that these changing conditions could also expand the ranges  
38 of some of these parasitic species. Thus, it is essential that the fishing industry effectively  
39 monitor fish tanks and water in the surrounding environments for the presence of  
40 zoosporic parasites including *I. chabelardi* in order to take steps to prevent large losses in  
41 these fisheries.

42

43

44

45 **Introduction**

46 **Objectives of this review**

47 This review focuses on the marine dinoflagellate parasite *Ichthyodinium chabelardi*  
48 Hollande & J. Cachon. The genus *Ichthyodinium* (Class Syndiniophyceae) consists of one  
49 species, *I. chabelardi*. This species is a virulent, generalist, endobiotic parasite of embryos  
50 and young larvae of many species of marine fin fish (Class Osteichthyes) living and  
51 reproducing in the ichthyoplankton, primarily in tropical and warm temperate oceanic  
52 ecosystems (Stratoudakis *et al.* 2000; Shadrin *et al.* 2010b). *I. chabelardi* has been  
53 intensively studied in only a few host fin fish species. Most of the fin fish which carry this  
54 parasite have been poorly investigated, even though some of the host fish species are  
55 economically important food resources. Because there is some evidence that the  
56 prevalence of other types of parasitic infections may increase with rising seawater  
57 temperatures (van West 2006; Gozlan *et al.* 2014; Ercan *et al.* 2015), it is extremely  
58 important to understand their mechanisms of infectivity, potential future distributions, and  
59 begin to explore approaches to mitigation before they become an even greater threat to  
60 fisheries.

61 Until now, no review of the literature on this parasite has been available. In contrast,  
62 several compilations have been written about a closely related host generalist parasitic  
63 protist belonging to the *Hematodinium* genus (also in the Class Syndiniophyceae)  
64 (Stentiford and Shields 2005; Small and Pagenkopp 2011). The infectious agent of the  
65 'bitter crab disease' (BCD) or the 'bitter crab syndrome' infects many commercially  
66 important host species around the world including crabs, lobsters and amphipods. This  
67 parasite has also been implicated in several outbreaks in fishery and aquaculture facilities  
68 leading to substantial annual economic losses (Shields 1994; Stentiford and Shields 2005;

69 Small *et al.* 2012). Given that *I. chabelardi* is also a generalist parasite infecting several  
70 different species of fish hosts with high prevalence levels, we predict that it, too, could  
71 have a significant impact on commercial fin fish populations.

72 In this review we firstly discuss the phylogeny, biology and ecology of *I. chabelardi*  
73 focusing on its morphology and life cycle and the pathology of its infections in host  
74 fishes. We then describe the putative geographical expansion and host shift of this  
75 emerging disease and its potential ecological roles in marine food webs. We briefly  
76 compare the biology of *I. chabelardi* with four other emerging zoosporic parasites which  
77 commonly infect fin fish: *Amyloodium ocellatum*, *Saprolegnia parasitica*, *Sphaerothecum*  
78 *destruens* and “X-cell” parasites. Finally, we appraise the future possibility of large losses  
79 in production of marine fin fish to epidemics in fish farms unless measures are  
80 implemented to prevent the spread of parasitic infections.

81

## 82 **Phylogenetic position of *Ichthyodinium chabelardi***

83 Baldauf (2003, 2008) divided all eukaryotic organisms into eight supergroups based upon  
84 consensus phylogeny. The supergroup Alveolata consists of a very diverse range of  
85 marine and freshwater protists belonging to three lineages: dinoflagellates, apicomplexans  
86 and ciliates. Presently the dinoflagellates (Phylum Dinozoa) include the following large  
87 clades based on both molecular and morphological characteristics: Phylum Perkinsozoa  
88 (Norén *et al.* 1999), Class Noctiluciphyceae (Gómez *et al.* 2010), Class Dinophyceae  
89 (core dinoflagellates) (Pascher 1914), and Class Syndiniophyceae (to which  
90 *Ichthyodinium chabelardi* belongs) (Loeblich III 1976). There are also several small  
91 clades, one of which includes the genus *Oxyrrhis* (Lowe *et al.* 2010).

92 Within the alveolates there are phototrophic, heterotrophic, and mixotrophic species. Most  
93 of the core dinoflagellates are thought to be photosynthetic (including mixotrophs), but  
94 there are also some heterotrophic species. Approximately half of all known dinoflagellate  
95 species in all classes taken as a group are heterotrophic (Lessard and Swift 1986). Some  
96 species of heterotrophic dinoflagellates contain plastids that lack a functional  
97 photosynthetic apparatus (Robledo *et al.* 2011). The Phylum Perkinsozoa, Class  
98 Syndiniophyceae, Class Blastodinophyceae, Class Noctiluciphyceae and the *Oxyrrhis*  
99 clade are all groups of heterotrophic protists which lack functional chloroplasts and have  
100 diverged into clades that are currently considered separate from the Class Dinophyceae  
101 (core dinoflagellates) (Gómez *et al.* 2010; Bachvaroff *et al.* 2014).

102 *I. chabelardi* belongs to Class Syndiniophyceae which is composed of diverse lineages of  
103 mainly endobiotic parasites, with several clades consisting entirely of uncultured species  
104 (Moon-Van der Staay *et al.* 2001; Guillou *et al.* 2008). The Syndiniales are exclusive to  
105 marine environments. Because of their endoparasitic lifestyle, they have unusual  
106 adaptations, making them almost unrecognizable as dinoflagellates when inside their  
107 hosts. The Syndiniales include at least five major marine alveolate (MALV) groups,  
108 typically referred to as MALV I, II, III, IV, and V (but sometimes interchangeably as  
109 Syndiniales I – V) (Guillou *et al.* 2008; Chambouvet *et al.* 2011). MALV II is currently  
110 recognized as the most diverse clade and contains some of the more thoroughly studied  
111 species, including numerous members of the genus *Amoebophrya*. Most members of  
112 MALV II have been identified as parasites of dinoflagellates, although some also infect  
113 radiolarians. Members of MALV IV infect other metazoans including *Hematodinium*, and  
114 *Syndinium*, two well-characterized parasites of crustaceans. MALV III and MALV V  
115 currently consist entirely of environmental sequences, but form well-supported clades

116 (Guillou *et al.* 2008). Finally, MALV I includes *Ichthyodinium* spp. as well as members  
117 that infect ciliates (Euduboscquellidae) (Coats 1988; Coats and Heisler 1989; Harada *et*  
118 *al.* 2007; Jung *et al.* 2016). A schematic representation of the position of MALV I relative  
119 to other members of Syndiniales and Dinophyceae is provided in Figure 1A.

120 *Ichthyodinium chabelardi* was originally described as a syndinid dinoflagellate by  
121 Hollande and Cachon (1952) with additional observations on its morphology and biology  
122 (Hollande and Cachon, 1953). Morphologically, *I. chabelardi* shares key features with  
123 other dinoflagellates. These include trichocysts, condensed chromatin in the nucleus of  
124 trophic stages, a dinospore (or zoospore) with two lateral flagella, and an alveolate pellicle  
125 synthesized inside alveolar membranes (Hollande and Cachon 1952; Gestal *et al.* 2006;  
126 Simdyanov *et al.* 2016).

127

128 The phylogenetic placement of *I. chabelardi* within the Alveolata superphylum remains  
129 controversial. Gestal *et al.* in 2006 using molecular methods placed this parasite at the  
130 base of the Perkinsozoa lineage, renaming the genus *Perkinsoide* (Gestal *et al.* 2006).  
131 However, analysis of the SSU and LSU regions show poor support for this change, and  
132 zoospore ultrastructure is more similar to other groups of dinoflagellates than the  
133 Perkinsozoa. As with recent authors (Mori *et al.* 2007; Skovgaard *et al.* 2009; Simdyanov  
134 *et al.* 2016), we retain the placement of *I. chabelardi* in the Syndiniophyceae until  
135 additional work is done on its taxonomic affinities.

136 Although only one species has been formally described thus far, genetic analysis of the  
137 SSU rDNA of the parasitic protists infecting a mix fish larvae of eight different species  
138 reveal slight differences in the sequences, which suggests that there could be at least two  
139 different ribotypes (98% of identity - 22 nt/ 868bp) in the sample (Sørensen *et al.* 2014).

140 These form separate clades within MALV I – 3 when aligned with other environmental  
141 SSU rDNA sequences (Figure 1B). These two ribotypes have been detected to date in  
142 distinct oceanic regions (Figure 2). These results provide the evidence that this group  
143 might be more complex than previously described and composed of genetically distinct  
144 parasites, as has been characterized for other syndinean parasites such as *Amoebophrya*  
145 spp. (Guillou *et al.* 2008).

146

147

#### 148 **Life cycle of *I. chabelardi***

149 *Ichthyodinium chabelardi* was originally described as an infectious agent of sardines from  
150 the Mediterranean Sea (Alger Bay) by Hollande and Cachon (1952), who made additional  
151 observations on its morphology and biology (Hollande and Cachon 1953). These  
152 descriptions reveal a complex life cycle that might differ depending on the parasite and/or  
153 host species, with infections in some hosts appearing to have two generations of schizonts  
154 while others have been observed with three (Figure 3). Subsequently, free-swimming  
155 zoospores are released which can then infect new hosts.

156 The first evidence of infection appears in the yolk sac of embryos after gastrulation  
157 (stages VI to XI, Dulčić 1998; Meneses *et al.* 2003). Infected eggs have no sign of  
158 penetration on their surface, suggesting that the parasite may pass through the hole for  
159 sperm penetration before the hole is completely closed (Yuasa *et al.* 2007).

160 Three successive stages of schizonts have been described by Hollande and Cachon (1953):

161 **Primordial schizonts:** The smallest stages of the parasite appear to be unicellular spheres  
162 (maximum 1 to 3 per egg) with a diameter of approximately 8-15  $\mu\text{m}$ , less than 20  $\mu\text{m}$



163 (Hollande and Cachon 1952, 1953; Meneses *et al.* 2003; Yuasa *et al.* 2007; Sorensen et al.  
164 2014). These trophocytes absorb the vitellus material of the host in a central vacuole and  
165 remain uni-nucleated, although mitotic divisions following by transversal divisions may  
166 occur at this stage. Then, the nucleus undergoes multiple mitotic divisions without  
167 subsequent cytoplasmic division and the primordial schizont rapidly becomes a large  
168 multinucleated structure of 100-140  $\mu\text{m}$ . The cytoplasm forms cylindrical projections  
169 around each nucleus and each of these units become a secondary schizont ( $\sim 20\text{-}30 \mu\text{m}$ )  
170 that eventually separates from the rest in a budlike manner.

171 **Secondary schizonts:** These are cylindrical or in a racket-like shape, about 20  $\mu\text{m}$  in  
172 length (Hollande and Cachon 1953). Lecithin starts to concentrate in these forms. This  
173 early secondary schizont first grows, then begins to divide by longitudinal bipartitions. As  
174 the posterior poles of the two daughter cells remain attached, the parasites assume a  
175 triangular form, resembling to a 'rosace'. Secondary schizonts can then form a long cord  
176 (up to 1–2 mm) in layers of successive groups of eight cells connected by their poles  
177 (Hollande and Cachon 1953).

178 **Last generation of schizonts:** Oblong (cylindrical) schizonts are released from the cord,  
179 which become spherical after a series of divisions. At this phase, the yolk sac is opaque  
180 and entirely occupied by uni-nucleated parasitic cells. This last generation of schizonts  
181 produce zoosporangia, which are released outside the host, in the water, generally after  
182 hatching. The yolk sac breaks causing the death of the newly hatched larvae. In some  
183 larvae, the parasite burst occurs immediately after hatching, while it takes more than 10 h  
184 after hatching in others (Mori *et al.* 2007). The number of sporangia released from a yolk-  
185 sac larva of the yellowfin tuna *Thunnus albacares* has been estimated to be about  $4 \times 10^4$   
186 cells (Yuasa *et al.* 2007).

187 In the water, the sporangia undergo one to two divisions and become flagellated (Hollande  
188 and Cachon 1953). These spores have trichocysts (Gestal *et al.* 2006), which are known to  
189 be involved in the host attachment in other Syndiniales (Miller *et al.* 2012). Nuclei of  
190 released spores exhibit numerous nuclear pores and have chromatin masses, permanently  
191 condensed in circular or oval profiles of DNA. In some cases, structures like rhoptries and  
192 microtubule-organizing centres, similar to specific apicomplexan characteristics, have  
193 been observed at this developmental phase (Gestal *et al.* 2006). These structures may have  
194 similar function during the host invasion as the dense bodies and striated strips observed  
195 in *Amoebophrya* (Miller *et al.* 2012). Spores remain actively swimming for a few days,  
196 but cannot survive in a free-living state beyond that (Hollande and Cachon 1953). Spores  
197 of different sizes (Skovgaard *et al.* 2009) seem to correspond to different generations of  
198 division (Shadrin *et al.* 2015). The fate of the parasite outside of the host is not known at  
199 present.

200 **Variations observed from this complex life cycle:** The three generations of schizonts,  
201 first described on sardines from the Mediterranean Sea, were also observed in the  
202 mackerel off Portugal (Meneses *et al.* 2003). However, secondary schizonts seem to be  
203 absent on sardines from Portugal (Borges *et al.* 1996; Gestal *et al.* 2006) and several other  
204 host species, such as *Plectropomus leopardus* from Japan (Mori *et al.* 2007) and *Thunnus*  
205 *albacore* (Yuasa *et al.* 2007). In this case, primary schizonts lead directly to the last  
206 generation schizonts, without producing the rosace and cord. No zoosporangium was  
207 formed in *Plectropomus leopardus* from Japan (Mori *et al.* 2007); instead, schizonts  
208 themselves transformed into zoospores within 10 minutes after release.

209

210 **Host range and geographical distribution**

211 Parasitic species appear to be highly ubiquitous in the world's oceans. Known parasites  
212 comprised more than half of both the richness and abundance of sequences within the  
213 pico-nanoplankton size fraction collected in the TARA Oceans expedition, which sampled  
214 at 68 stations across the world's oceans (de Vargas *et al.* 2015). Within the TARA study,  
215 the Syndiniales featured prominently and over 2000 species-level OTUs were assigned to  
216 the MALV I clade (which includes *Ichthyodinium* spp.). Additionally, parasitic  
217 interactions were the most common type of interaction identified from network analysis of  
218 this global sequence dataset (Lima-Mendez *et al.* 2015).

219 There is evidence that parasitism by certain Syndiniales species could play a role in  
220 regulating the populations of their hosts. This has even been suggested as a means of  
221 controlling harmful algal blooms since many toxic dinoflagellates have been identified as  
222 Syndiniales hosts (Taylor 1968). In the Penzé estuary in France, Chambouvet *et al.* (2008)  
223 consistently found successive blooms and declines of four different dinoflagellate species,  
224 with prevalence of different Syndiniales species corresponding to or shortly lagging each  
225 of the four dinoflagellate blooms. It is clear that in certain cases Syndiniales species can  
226 heavily impact the dynamics of their host populations, and given the incredible diversity  
227 of hosts, their regulatory effects on a wide range of marine organisms, including fishes,  
228 are understudied.

229 Microscopic and molecular analysis of pelagic samples of ichthyoplankton have revealed  
230 the presence of *I. chabelardi* and relatives in the yolk sacs of fertilized eggs, embryos and  
231 larvae in various species of fish at widely distributed sites in the South China Sea (Shadrin  
232 *et al.* 2010 a and b), South Pacific (Yuasa *et al.* 2007) and in the North Eastern Atlantic  
233 and the Mediterranean (Dulčić 1998; Skovgaard *et al.* 2009). Up to now, *I. chabelardi* is  
234 reported to infect at least 13 different marine fish species including several commercially

235 important species such as *Maurolicus muelleri* (Guelin) and *Sparus aurata* L., *Trachurus*  
236 *trachurus* L., *Micromeesistius poutassou* (Risso) and *Engraulis encrasicolus* L. and  
237 *Scophthalmus morhua* L. (see Table 1 for more details on observations in certain host  
238 species, Figure 2 for geographical distribution, and the Aquasymbio website:  
239 <http://www.aquasymbio.fr/fr>).

240 The presence of this pathogen has not been reported elsewhere in the ocean in wild host  
241 fish species but has become a pest in some fish farms (Mori *et al.* 2007; Yuasa *et al.*  
242 2007). No data has been collected for the prevalence of *I. chabelardi* at most other sites at  
243 which general surveys for dinoflagellates have been conducted. Most sampling sites  
244 where *I. chabelardi* has been detected have been in warm water. The only surveys in cold  
245 water were near Denmark (Sørensen *et al.* 2014). It is therefore clear that *I. chabelardi*  
246 and relatives are generalist parasites infecting many bony fish species and are widely  
247 distributed throughout the oceans. However, most of the studies thus far focus on few  
248 ecosystems and broader surveys are required today to establish the global distribution of  
249 these parasites.

250

### 251 **Infectivity and ecological significance**

252 The prevalence of *Ichthyodinium* parasites in ichthyoplankton samples has been  
253 investigated in various euphotic zones (North Atlantic, Mediterranean, South China and  
254 South Pacific waters). These shorter-term studies highlight a surprisingly high prevalence  
255 (Pedersen *et al.* 1994; Stratoudakis *et al.* 2000; Skovgaard *et al.* 2009). For example, field  
256 studies in the North Atlantic revealed infection prevalences of 37% in sardine eggs in  
257 1999 and 46% in mackerel eggs in 2000 (Stratoudakis *et al.* 2000; Meneses *et al.* 2003).

258 In the South Pacific the prevalence was nearly 100% for yellow fin tuna in 2007 (Yuasa *et*  
259 *al.* 2007).

260 More recently, Shadrin *et al.* (2010b) confirm this high prevalence at Nha Trang Bay,  
261 Vietnam between 2001 and 2010 detecting *Ichthyodinium*-like parasite in representatives  
262 of eight families of fish. These long-term observations reveal also an increase of parasitic  
263 prevalence year after year leading to a substantial proportion of fish mortality at early  
264 developmental stages. Hence, infection prevalence was no more than 1% in 1993, but  
265 reached up to 98% in 2006. Similarly, a recent study on the leopard coral grouper fish in  
266 southern Japan reveal that parasitic prevalence attributed to *Ichthyodinium* sp. ranged in  
267 the same batch from 1.9% in 1990 to 31.8% in 1995 (Mori *et al.* 2007).

268 Shadrin *et al.* (2010a) have suggested that infection by *I. chabelardi* has been responsible  
269 for the significant disappearance of populations of fish species in warm water off the coast  
270 of Vietnam. The quantitative effect of infection by this parasite elsewhere awaits further  
271 long-term investigation. However, present data suggest that *I. chabelardi* is an emerging  
272 pathogen and is spreading into new marine ecosystems and possibly into freshwater  
273 ecosystems (Sørensen *et al.* 2014).

274 Taken all together, these findings data suggest that the impact of this parasite on fish host  
275 populations is still today underestimated and long-term investigation is urgently needed.

276

### 277 **Other emerging eukaryotic parasites of fish**

278 *Ichthyodinium chabelardi* is not alone in its role as an emerging threat to fisheries. Several  
279 other protists of differing phylogenetic origins, and different life cycles and modes of

280 infection, also present a challenge for fishery management. Here we briefly describe the  
281 mechanisms and effects of five other eukaryotic parasites.

282 *Amyloodium ocellatum* (Class Dinophyceae, Order Peridiniales) is known to infect over  
283 100 species of fin fish worldwide causing marine velvet disease or amyloodiniosis  
284 (Landsberg *et al.* 1994, see also the Aquasymbio website: <http://www.aquasymbio.fr/fr>).  
285 *A. ocellatum* is a virulent euryhaline ectobiotic parasite that tolerates varying osmotic  
286 conditions and temperatures and is commonly observed in warm and temperate oceanic  
287 environments including coral reefs and especially in crowded fish pens and aquaria (Noga  
288 1989; Levy *et al.* 2007). This species can grow at temperatures of up to 40 °C (Kuperman  
289 and Matey 1999). The details of its life cycle have been worked out, and there do appear  
290 to be seasonal, temperature-related dynamics of infection prevalence (Kuperman and  
291 Matey 1999). Its free-swimming dinospore stage attaches to the gills and skin of hatched  
292 fish (Kuperman and Matey 1999) rather than the eggs as does *I. chabelardi*.

293 *Saprolegnia parasitica* (Phylum Oomycota) and *Sphaerothecum destruens* (Phylum  
294 Mesomycetozoa) are known to be significant emerging parasites and are very serious  
295 threats for production in populations of both wild and farmed fin fish in freshwater  
296 ecosystems (van West 2006; Rowley *et al.* 2013; Gozlan *et al.* 2014; Sarowar *et al.* 2014).  
297 Both species have been spread widely by resistant carriers into new ecosystems where  
298 these pathogens have formerly never been observed.

299 Several pathotypes of *Saprolegnia* can act as opportunistic and aggressive parasites of  
300 egg, larval and adult stages of many economically important species of fish such as  
301 salmon, trout and catfish, and are responsible for significant economic losses in salmon  
302 hatcheries. Thoen *et al.* (2015) found many different ITS-based genotypes among 89

303 isolates of *Saprolegnia* recovered from water samples and egg, larval and adult salmon  
304 tissues from 26 salmon hatcheries along the coast of Norway. A limited number of species  
305 of *Saprolegnia* (four species) were found in tissues of salmon: *diclina*, *ferax*, *hypogyra*  
306 and *parasitica*. *S. diclina* (sub-clade IIIB) clearly dominated and accounted for 79% of the  
307 recovered species. These data indicate considerable genetic variation within the  
308 populations of *Saprolegnia* pathogens, but the relationship to pathogenicity is not known.

309 *Sphaerothecum destruens* was spread from China to Europe by a healthy freshwater  
310 carrier species, the top-mouth gudgeon (*Pseudorasbora parva*) (Gozlan, 2014). Recently  
311 the rate of spread within parts of Europe has been estimated to be very rapid (Ercan *et al.*  
312 2015). This pathogen is a generalist, can infect a wide range of hosts and can cause high  
313 mortalities, especially in commercially important fish species such as Chinook salmon  
314 (*Oncorhynchus tshawytscha*) and Atlantic salmon (*Salmo salar*).

315 **The “X-cell” clades *Gadixcellia* and *Xcellia*** (Superphylum Alveolata) are parasites  
316 associated with tumor-like formations in teleost fishes, including several groups of  
317 commercial interest (Freeman *et al.* 2017). X-cells were originally believed to be  
318 abnormal, diseased host cells, but cells extracted from lesions in the gills and skin of  
319 various fishes reveal them to be a related group of parasitic protists. The phylogeny of  
320 these parasites is newly characterized and shows an unexpected level of divergence  
321 between the two robust x-cell clades within the Phylum Perkinsozoa (Alveolata). Both  
322 clades are basal to the Perkinsids. Fishes with x-cell infections have been observed in the  
323 Atlantic, Pacific, and Southern oceans (Evans and Tupmongkol 2014; Freeman *et al.*  
324 2017), but the parasites have not yet been observed, nor their sequences detected, in  
325 seawater independently of their hosts. In the common dab, diseased fish had difficulty  
326 with respiration and much lower survival than healthy fish (Diamant and Vicar 1987).

327 It is clear that *Ichthyodinium chabelardi* is not the only infectious disease threatening the  
328 future survival of important fisheries. Many diseases have been described. Moreover,  
329 eukaryotic parasites have been under-studied and neglected so far despite their major role  
330 in fish disease. Some methods have been proposed to control the spread of these parasites  
331 in controlled environments including reduced salt concentration and various chemicals,  
332 though some of these (like malachite green) have been banned due to their toxicity to  
333 humans (van West 2006). Further knowledge of each of these parasites, especially their  
334 early detection and predicted responses to changing ocean conditions, will be of crucial  
335 importance to the future of fish production.

336

### 337 **Future perspectives and conclusions**

338 There are plans in the future to build new hatcheries for production of marine fin fish  
339 species such as cod along the coasts where appropriate. Countries such as Norway,  
340 Scotland, Canada and southern Australia currently have only salmon hatcheries filled with  
341 cold freshwater. These facilities could be easily modified for marine fish using cold  
342 seawater. However, a dramatic increase of disease caused by *Saprolegnia* in freshwater  
343 fish tanks has already been observed (van West 2006). This appears to be a result of two  
344 factors: the mean temperature of the ocean is predicted to increase significantly with  
345 global warming, and furthermore the use of malachite green in the tanks to prevent the  
346 growth of parasites has been banned internationally because of its toxicity to humans (van  
347 West 2006).

348 It is often concluded that geographical range and prevalence of emerging infectious  
349 diseases has increased tremendously over the last 20 years (Harvell 1999, 2002; Sutherst



350 2001). Climate change, habitat destruction, and introduction of exotic species (hosts and  
351 parasites) have been blamed for this increase. Actually, it has recently been observed that  
352 the combination of introduction of diseased fish with the rise of seawater temperature has  
353 significantly increased the prevalence of diseases of fin fish in general (van West 2006;  
354 Gozlan 2014; Ercan *et al.* 2015). We therefore predict that the ocean temperature increase  
355 will provide more favourable environmental conditions for parasite growth and will  
356 inexorably lead to geographical expansion of infectious agent populations like *I.*  
357 *chabelardi* and other protozoan parasites. This movement could impact population  
358 dynamics and may drive a decrease of or even cause extinction of commercially important  
359 fish population stock. It is not known whether fish could have a designated area to provide  
360 protection from infection by this parasite, but cold water in the oceans near the poles  
361 could be a reservoir if there is sufficient oxygen present.

362 It is essential that the fishing industry effectively monitor fish tanks and water in the  
363 surrounding environments for the presence of parasites and takes steps to prevent large  
364 losses in fish production. At present efforts to measure the prevalence of these parasites  
365 appear to be inadequate. Molecular methods may provide tools for early detection (for  
366 example, PCR of environmental samples using *Ichthyodinium*-specific primers), but  
367 further research is required to develop new procedures for monitoring and controlling  
368 infections. Mori *et al.* (2007) were able to prevent horizontal transfer of infection by using  
369 UV-sterilized or ozone-treated seawater. Methods such as these might warrant further  
370 exploration for fish tank settings.

371 Pathogenic species such as *I. chabelardi* and the others discussed in this paper infect a  
372 wide variety of host species that may favor their spread. Generalist parasites have been  
373 responsible for huge losses in populations of plants and animals in agriculture,

374 aquaculture and the environment (Phillips *et al.* 2008). All of the species discussed in this  
375 review are examples of emerging pathogens and equally important to the economy of the  
376 aquaculture industry (Stentiford *et al.* 2012) in a world in which food production must be  
377 increased to keep up with human population growth. They are all spread easily and  
378 rapidly by highly infective free-living stage the zoospores from infected to uninfected  
379 susceptible host species of fish and could cause epidemics especially in highly dense host  
380 populations such as in fish farms.

381

## 382 **Figure Legends**

383

384 **Figure 1.** (A) Generalized schematic of Dinophyceae phylogeny with designation of the  
385 five major clades within Syndiniales. MALV I, to which *Ichthyodinium* spp. belong, is  
386 highlighted. Adapted from Guillou *et al.* 2008. (B) Partial SSU rDNA phylogeny  
387 (Maximum Likelihood) of *Ichthyodinium* spp. together with closely related environmental  
388 sequences (MALV I clade 3, following the nomenclature by Guillou *et al.* 2008), showing  
389 the two clusters described within the genus. Environmental sequences are labeled by their  
390 GenBank accession number following by the name of the clone. Sequences were retrieved  
391 from GenBank using BLAST and aligned with referenced *Ichthyodinium* spp. sequences  
392 using the online version of MAFFT version 7 (<https://mafft.cbrc.jp/alignment/server/>), and  
393 considering the secondary structure of RNA. RAxML (Randomized Axelerated Maximum  
394 Likelihood) was performed using the GTRCAT substitution model, using a random  
395 number seeds, and 100 replicates for the bootstrap analyses.

396

397 **Figure 2.** Known global distributions and hosts of the two established ribotypes of  
398 *Ichthyodinium* sp.

399

400 **Figure 3.** Life cycle of *I. chabelardi* as observed in mackerel eggs (from Meneses et al.  
401 2003).

402

403 **Table 1.** Some examples of pathotypes of *Ichthyodinium chabelardi* reported as parasites  
404 of fish species. Recently identities have been confirmed by both light microscopic studies  
405 and molecular methods.

406

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414

415 **Conflict of Interest**

416 The authors declare no conflict of interest.

417 **References**

418 Bachvaroff, T. R., S. G. Gornik, G. T. Concepcion, R. F. Waller, G. S. Mendez, J. C.

419 Lippmeier, and Delwiche, C. F. (2014). Dinoflagellate phylogeny revisited: using

420 ribosomal proteins to resolve deep branching dinoflagellate clades. *Molecular*

421 *Phylogenetics and Evolution* **70**, 314-322.

422

423 Baldauf, S. L. (2003). The deep route of Eukaryotes. *Science* **300**, 1703-1706.

424

425 Baldauf, S. L. (2008). An overview of the phylogeny and diversity of eukaryotes. *Journal*

426 *of Systematics and Evolution* **46**, 263-273.

427

428 Borges, R., Ré, P. and Azevedo, C. (1996). *Ichthyodinium chabelardi* (Hollande e Cachon

429 1952), dinoflagelado parasita dos ovos de sardinha. *Ciência Biológica. Ecology and*

430 *Systematics (Portugal)* **16**, 245–258.

431

432 Chambouvet, A., Morin, P., Marie, D. and Guillou, L. (2008). Control of toxic marine

433 dinoflagellate blooms by serial parasitic killers. *Science* **322(5905)**, 1254-1257.

434

435 Chambouvet, A., Alves-de-Souza, C., Cueff, V., Marie, D., Karpov, S., and Guillou, L.

436 (2011). Interplay between the parasite *Amoebophrya* sp. (Alveolata) and the cyst

437 formation of the red tide dinoflagellate *Scrippsiella trochoidea*. *Protist* **162(4)**, 637-649.

438

439 Coats, D. W. (1988). *Duboscquella cachoni* n. sp., a parasitic dinoflagellate lethal to its  
440 tintinnine host *Eutintinnus pectinis*. *The Journal of Protozoology* 35(4), 607-617.

441

442 Coats, D. W., and Heisler, J. J. (1989). Spatial and temporal occurrence of the parasitic  
443 dinoflagellate *Duboscquella cachoni* and its tintinnine host *Eutintinnus pectinis* in  
444 Chesapeake Bay. *Marine Biology* **101(3)**, 401-409..

445

446 De Vargas, C., Audic, S., Henry, N., Decelle, J., Mahé, F., Logares, R., Lara, E., Berney,  
447 C., Le Bescot, N., Probert, I. and Carmichael, M. (2015). Eukaryotic plankton diversity in  
448 the sunlit ocean. *Science* **348(6237)**, 1261605.

449

450 Diamant, A., and McVicar, A. H. (1987). The effect of internal and external X-cell lesions  
451 on common dab, *Limanda limanda* L. *Aquaculture* **67(1-2)**, 127-133.

452

453 Dulčić, J. (1998). Infection of sardine eggs by a parasitic dinoflagellate *Ichthyodinium*  
454 *chabelardi* Hollande and Cachon, 1952 in Croatian waters. *Annales: anali za istrske in*  
455 *mediteranske študije. Series historia naturalis* **13**, 15-18.

456

457 Ercan, D., Andreou, D., Sana, S., Öntaş, C., Baba, E., Top, N., Karakuş, U., Tarkan, A.S.  
458 and Gozlan, R.E. (2015). Evidence of threat to European economy and biodiversity

459 following the introduction of an alien pathogen on the fungal–animal boundary. *Emerging*  
460 *microbes & infections* **4(9)**, 52.

461

462 Evans, C. W., and Tupmongkol, K. (2014). X-cell disease in Antarctic fishes. *Polar*  
463 *biology* **37(9)**, 1261-1269.

464

465 Freeman, M.A., Fuss, J., Kristmundsson, A., Bjorbækmo, M.F., Mangot, J.F., del Campo,  
466 J., Keeling, P.J., Shalchian-Tabrizi, K. and Bass, D. (2017). X-Cells Are Globally  
467 Distributed, Genetically Divergent Fish Parasites Related to Perkinsids and  
468 Dinoflagellates. *Current Biology*, **27(11)**, 1645-1651.

469

470 Gestal, C., Novoa, B., Posada, D., Figueras, A., and Azevedo, C. (2006). *Perkinsoide*  
471 *chabelardi* n. gen., a protozoan parasite with an intermediate evolutionary position:  
472 possible cause of the decrease of sardine fisheries?. *Environmental microbiology* **8(6)**,  
473 1105-1114.

474

475 Gómez, F., Moreira, D., and López-García, P. (2010). Molecular phylogeny of noctiluroid  
476 dinoflagellates (Noctilucales, Dinophyceae). *Protist* **161(3)**, 466-478.

477

478 Gozlan, R. E., Marshall, W., Lilje, O., Jessop, C., Gleason, F. H., and Andreou, D. (2014).  
479 Current ecological understanding of fungal-like pathogens of fish: what lies beneath?  
480 *Frontiers in microbiology*, **5**, 62.  
481  
482 Guillou, L., Viprey, M., Chambouvet, A., Welsh, R.M., Kirkham, A.R., Massana, R.,  
483 Scanlan, D.J. and Worden, A.Z. (2008). Widespread occurrence and genetic diversity of  
484 marine parasitoids belonging to Syndiniales (Alveolata). *Environmental Microbiology*,  
485 **10(12)**, 3349-3365.  
486  
487 Harada, A., Ohtsuka, S., and Horiguchi, T. (2007). Species of the parasitic genus  
488 *Duboscquella* are members of the enigmatic Marine Alveolate Group I. *Protist* **158(3)**,  
489 337-347.  
490  
491 Harvell, C.D., Kim, K., Burkholder, J.M., Colwell, R.R., Epstein, P.R., Grimes, D.J.,  
492 Hofmann, E.E., Lipp, E.K., Osterhaus, A.D.M.E., Overstreet, R.M. and Porter, J.W.  
493 (1999). Emerging marine diseases--climate links and anthropogenic factors. *Science*  
494 **285(5433)**, 1505-1510.  
495  
496 Harvell, C. D., Mitchell, C. E., Ward, J. R., Altizer, S., Dobson, A. P., Ostfeld, R. S., and  
497 Samuel, M. D. (2002). Climate warming and disease risks for terrestrial and marine biota.  
498 *Science* **296(5576)**, 2158-2162.  
499  
500 Hollande, A. and Cachon, J. (1952). Un parasite des oeufs de sardine: l'*Ichthyodinium*  
501 *chabelardi*, nov. gen., nov. sp. *CR Acad. Sci., Paris (Ser. D)* **235**, 976-977.  
502



503 Hollande, A. and Cachon, J. (1953). Morphologie et évolution d'un Péridinien parasite des  
504 oeufs de sardine (*Ichthyodinium chabelardi*). *Sta. Aquat. Pêches Ceutaglione* **4**, 321-331.  
505

506 Ishimaru, K., Iida, N., Okada, T., and Miyashita, S. (2012). *Ichthyodinium* infection in the  
507 embryos and yolk sac larvae of Pacific bluefin tuna *Thunnus orientalis*. *Fish Pathology*,  
508 **47(4)**, 143-146.  
509

510 Jung, J. H., Choi, J. M., Coats, D. W., and Kim, Y. O. (2016). *Euduboscquella costata* n.  
511 sp.(Dinoflagellata, Syndinea), an intracellular parasite of the ciliate *Schmidingerella*  
512 *arcuata*: morphology, molecular phylogeny, life cycle, prevalence, and infection intensity.  
513 *Journal of Eukaryotic Microbiology* **63(1)**, 3-15.  
514

515 Kuperman, B. I., and Matey, V. E. (1999). Massive infestation by *Amyloodinium*  
516 *ocellatum* (Dinoflagellida) of fish in a highly saline lake, Salton Sea, California, USA.  
517 *Diseases of Aquatic Organisms* **39(1)**, 65-73.  
518

519 Landsberg, J. H., Steidinger, K. A., Blakesley, B. A., and Zondervan, R. L. (1994).  
520 Scanning electron microscope study of dinospores of *Amyloodinium cf. ocellatum*, a  
521 pathogenic dinoflagellate parasite of marine fish, and comments on its relationship to the  
522 Peridinales. *Diseases of Aquatic Organisms* **20**, 23-32.  
523

524 Lessard, E. J., and Swift, E. (1986). Dinoflagellates from the North Atlantic classified as  
525 phototrophic or heterotrophic by epifluorescence microscopy. *Journal of Plankton*  
526 *Research* **8(6)**, 1209-1215.

527

528 Levy, M. G., Poore, M. F., Colorni, A., Noga, E. J., Vandersea, M. W., and Litaker, R. W.  
529 (2007). A highly specific PCR assay for detecting the fish ectoparasite *Amyloodinium*  
530 *ocellatum*. *Diseases of aquatic organisms* **73(3)**, 219-226.

531

532 Lima-Mendez, G., Faust, K., Henry, N., Decelle, J., Colin, S., Carcillo, F., Chaffron, S.,  
533 Ignacio-Espinosa, J.C., Roux, S., Vincent, F. and Bittner, L. (2015). Determinants of  
534 community structure in the global plankton interactome. *Science* **348(6237)**, 1262073.

535

536 Loeblich, A. R. (1976). Dinoflagellate evolution: speculation and evidence. *Journal of*  
537 *Eukaryotic Microbiology* **23(1)**, 13-28.

538

539 Lowe, C. D., Keeling, P. J., Martin, L. E., Slamovits, C. H., Watts, P. C., and Montagnes,  
540 D. J. (2010). Who is *Oxyrrhis marina*? Morphological and phylogenetic studies on an  
541 unusual dinoflagellate. *Journal of Plankton Research* **33(4)**, 555-567.

542

543 Meneses, I., Vendrell, C., and Stratoudakis, Y. (2003). Mackerel (*Scomber scombrus*)  
544 eggs parasitized by *Ichthyodinium chabelardi* in the north-east Atlantic: an overlooked  
545 source of mortality. *Journal of plankton research* **25(9)**, 1177-1181.

546

547 Miller, J. J., Delwiche, C. F., and Coats, D. W. (2012). Ultrastructure of *Amoebophrya* sp.  
548 and its changes during the course of infection. *Protist* **163(5)**, 720-745.

549

550 Moon-van der Staay, S. Y., De Wachter, R., and Vaulot, D. (2001). Oceanic 18S rDNA  
551 sequences from picoplankton reveal unsuspected eukaryotic diversity. *Nature* **409(6820)**,  
552 607.

553

554 Mori, K.I., Yamamoto, K., Teruya, K., Shiozawa, S., Yoseda, K., Sugaya, T., Shirakashi,  
555 S., Itoh, N. and Ogawa, K. (2007). Endoparasitic dinoflagellate of the genus  
556 *Ichthyodinium* infecting fertilized eggs and hatched larvae observed in the seed production  
557 of leopard coral grouper *Plectropomus leopardus*. *Fish Pathology* **42(1)**, 49-57.

558

559 Noga, E. J. (1989). Culture conditions affecting the in vitro propagation of *Amyloodinium*  
560 *ocellatum*. *Diseases of Aquatic Organisms* **6(2)**, 137-143.

561

562 Norén, F., Moestrup, Ø., and Rehnstam-Holm, A. S. (1999). *Parvilucifera infectans*  
563 Norén et Moestrup gen. et sp. nov.(Perkinsozoa phylum nov.): a parasitic flagellate  
564 capable of killing toxic microalgae. *European journal of protistology* **35(3)**, 233-254.

565

566 Pascher, A. (1914). Über flagellaten und algen. *Deutsche Botanische Gesellschaft*,  
567 *Berichte* **32**, 136-160.

568

569 Pedersen, B. H., and Kjøie, M. (1994). A protistan endoparasite in embryos and yolk-sac  
570 larvae of cod *Gadus morhua* and turbot *Scophthalmus maximus*. *Diseases of Aquatic*  
571 *Organisms* **19**, 39-46.

572

573 Phillips, A. J., Anderson, V. L., Robertson, E. J., Secombes, C. J., and Van West, P.  
574 (2008). New insights into animal pathogenic oomycetes. *Trends in microbiology* **16(1)**,  
575 13-19.

576

577 Robledo, J. A. F., Caler, E., Matsuzaki, M., Keeling, P. J., Shanmugam, D., Roos, D. S.,  
578 and Vasta, G. R. (2011). The search for the missing link: a relic plastid in Perkinsus?.  
579 *International journal for parasitology* **41(12)**, 1217-1229.

580

581 Rowley, J. J., Gleason, F. H., Andreou, D., Marshall, W. L., Lilje, O., and Gozlan, R.  
582 (2013). Impacts of mesomycetozoean parasites on amphibian and freshwater fish  
583 populations. *Fungal Biology Reviews* **27(3-4)**, 100-111.

584

585 Sarowar, M. N., Saraiva, M., Jessop, C. N., Lilje, O. Gleason, F. H. and van West, P.  
586 (2014). Infection strategies of pathogenic oomycetes in fish. In: 'Freshwater fungi and  
587 fungus-like organisms.' (Eds E. B. G. Jones, K-L. Pang, L. D. Hyde.) pp. 217-244. De  
588 Gruyter: Berlin, Germany.

589

590 Shadrin, A. M., Kholodova, M. V., and D. S. Pavlov. 2010a. Geographical distribution  
591 and molecular genetic identification of the parasite of the genus *Ichthyodinidium* causing

592 mass mortality of fish eggs and larvae in coastal waters of Vietnam. *Doklady Biological*  
593 *Sciences* **432**, 220-223.

594

595 Shadrin, A. M., Pavlov, D. S., and Kholodova, M. V. (2010b). Long-term dynamics of  
596 infection of fish eggs and larvae with the endoparasite *Ichthyodinium* sp. (Dinoflagellata)  
597 in Nha Trang Bay, Vietnam. *Fish Pathology* **45**, 103-108.

598

599 Shadrin, A. M., Simdyanov, T. G., Pavlov, D. S., and Nguyen, T. H. T. (2015). Free-  
600 living stages of the life cycle of the parasitic dinoflagellate *Ichthyodinium chabelardi*  
601 Hollande et J. Cachon, 1952 (Alveolata: Dinoflagellata). *Doklady Biological Sciences*  
602 **461(1)**, 104-107.

603

604 Shields, J. D. (1994). The parasitic dinoflagellates of marine crustaceans. *Annual Review*  
605 *of Fish Diseases* **4**, 241-271.

606

607 Simdyanov, T. G., Shadrin, A. M., and Thanh, N. T. H. (2016). The ultrastructure of the  
608 zoospores of the parasitic dinoflagellate *Ichthyodinium chabelardi* Hollande et J. Cachon,  
609 1952 (Alveolata: Dinoflagellata). *Doklady Biological Sciences* **468(1)**, 125-128.

610

611 Skovgaard, A., Meneses, I., and Angélico, M. M. (2009). Identifying the lethal fish egg  
612 parasite *Ichthyodinium chabelardi* as a member of Marine Alveolate Group I.  
613 *Environmental microbiology* **11(8)**, 2030-2041.

614

615 Skovgaard, A., Meyer, S., Overton, J. L., Støttrup, J., and Buchmann, K. (2010).  
616 Ribosomal RNA gene sequences confirm that protistan endoparasite of larval cod *Gadus*  
617 *morhua* is *Ichthyodinium* sp. *Diseases of aquatic organisms*, **88(2)**, 161-167.

618

619 Small, H. J., and Pagenkopp, K. M. (2011). Reservoirs and alternate hosts for pathogens  
620 of commercially important crustaceans: a review. *Journal of invertebrate pathology*  
621 **106(1)**, 153-164.

622

623 Small, H. J., Shields, J. D., Reece, K. S., Bateman, K., and Stentiford, G. D. (2012).  
624 Morphological and molecular characterization of *Hematodinium perezii* (Dinophyceae:  
625 Syndiniales), a dinoflagellate parasite of the harbour crab, *Liocarcinus depurator*. *Journal*  
626 *of Eukaryotic Microbiology* **59(1)**, 54-66.

627

628 Sørensen, S. R., Tomkiewicz, J., and Skovgaard, A. (2014). *Ichthyodinium* identified in  
629 the eggs of European eel (*Anguilla anguilla*) spawned in captivity. *Aquaculture* **426**, 197-  
630 203.

631

632 Stentiford, G. D., and Shields, J. D. (2005). A review of the parasitic dinoflagellates  
633 *Hematodinium* species and *Hematodinium*-like infections in marine crustaceans. *Diseases*  
634 *of aquatic organisms* **66(1)**, 47-70.

635

636 Stentiford, G.D., Neil, D.M., Peeler, E.J., Shields, J.D., Small, H.J., Flegel, T.W., Vlak,  
637 J.M., Jones, B., Morado, F., Moss, S. and Lotz, J. (2012). Disease will limit future food  
638 supply from the global crustacean fishery and aquaculture sectors. *Journal of invertebrate*  
639 *pathology* **110(2)**, 141-157.

640

641 Stratoudakis, Y., Barbosa, A., and Meneses, I. (2000). Infection of sardine eggs by the  
642 protistan endoparasite *Ichthyodinium chabelardi* off Portugal. *Journal of fish biology*  
643 **57(2)**, 476-482.

644

645 Sutherst, R. W. (2001). The vulnerability of animal and human health to parasites under  
646 global change. *International journal for parasitology* **31(9)**, 933-948.

647

648 Taylor, F. J. R. (1968). Parasitism of the toxin-producing *dinoflagellate* *Gonyaulax*  
649 *catenella* by the endoparasitic dinoflagellate *Amoebophrya ceratii*. *Journal of the*  
650 *Fisheries Board of Canada* **25(10)**, 2241-2245.

651

652 Thoen, E., Vrålstad, T., Rolén, E., Kristensen, R., Evensen, Ø., and Skaar, I. (2015).  
653 *Saprolegnia* species in Norwegian salmon hatcheries: field survey identifies *S. diclina*  
654 sub-clade IIIB as the dominating taxon. *Diseases of aquatic organisms* **114(3)**, 189-198.

655

656 Van West, P. (2006). *Saprolegnia parasitica*, an oomycete pathogen with a fishy appetite:  
657 new challenges for an old problem. *Mycologist* **20(3)**, 99-104.

658

659 Yuasa, K., Kamaishi, T., Mori, K. I., Hutapea, J. H., Permana, G. N., and Nakazawa, A.  
660 (2007). Infection by a protozoan endoparasite of the genus *Ichthyodinium* in embryos and  
661 yolk-sac larvae of yellowfin tuna *Thunnus albacares*. *Fish Pathology* **42(1)**, 59-66.

662

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