

1 Impacts of jellyfish on marine cage aquaculture: existing
2 knowledge and challenges to finfish health.

3 An overview of existing knowledge and challenges to aquaculture from cnidarian
4 zooplankton, with a focus on the medusoid stages known commonly as ‘jellyfish’.

5

6 Keywords: fish health, Cnidaria, mariculture, gill disease, zooplankton, net pen, Atlantic
7 salmon, sea bass.

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27 **Figure 1** Geographical distribution of jellyfish species of concern to aquaculture production.

28 **Table 1** Top marine finfish aquaculture producers globally.

29 **Figure 2** Histological sections of cnidarian impact in fish tissues.

30 **Figure 3** The jellyfish challenge to aquaculture: Varied impacts on fish health from

31 Coelenterata.

32 **Figure 4** Clinical consequences of jellyfish exposure.

33 **Table 2** Gelatinous plankton associated with impaired finfish health; Documented densities

34 and consequences to fish.

35

36 **Abstract**

37

38 Increasing conflict between gelatinous plankton and marine caged production of fish presents

39 a challenge to aquaculture that remains to be addressed. Shifting plankton distributions,

40 suggested by some to be as a result of factors such as climate change, appear to be further

41 exacerbated by anthropogenic factors linked directly to aquaculture. Of the gelatinous

42 plankton documented as harmful to marine fish production, it is the cnidarians that appear

43 particularly problematic, based at least partially on their ability to sting. Existing literature

44 illustrates the consequences to fish from the cnidarian hydrozoan and scyphozoan life-stages

45 commonly referred to as ‘jellyfish’. This impact is particularly pronounced in gill tissue,

46 where three key negative impacts are identified as a consequence of exposure; direct

47 traumatic damage to tissue, impaired function including oxygen deprivation, and initiation of

48 secondary disease (possibly through vector transmission via the ‘dirty needle’ of a microbe-

49 coated sting). Cnidarian jellyfish that have been demonstrated experimentally to negatively

50 impact fish include *Cyanea capillata*, *Aurelia aurita* and *Pelagia noctiluca*. Sessile polyps of
51 species such as *Ectopleura larynx* are also problematic. The available literature associates a
52 number of further coelenterates with harm to fish in the marine cage environment too. An
53 accurate picture of inshore planktic populations and exposure densities within the coastal
54 environments used for aquaculture is however presently lacking. This information would aid
55 in understanding cnidarian species of concern, and their role in impaired fish health,
56 particularly gill disease.

57

58 This review summarises the recent literature regarding the impact of gelatinous plankton on
59 finfish aquaculture, with a focus on cnidarian impact on fish health. Present strategies in
60 monitoring and mitigation are presented alongside identified critical knowledge gaps.

61

62 **1. Introduction**

63

64 With increasing demand for seafood that cannot be met through sustainable harvest of wild
65 fisheries alone, aquaculture production will be vital for human food security (FAO, 2019;
66 Costello *et al.*, 2020). Aquaculture continues to expand availability of fish, with marine
67 finfish contributing approximately 25% of the total estimated \$139.7 billion (USD) value of
68 global aquaculture (FAO, 2020). Though methods of production vary across many species of
69 fish, there are universal industry challenges. Other than in self-contained recirculating
70 aquaculture systems (RAS), exclusion of infectious and harmful agents of disease presents a
71 constant challenge (Kent *et al.*, 2009). Many challenges appear to disproportionately impact
72 cage-held fish over wild stocks, likely due to factors such as fish confinement, high stocking
73 density, and the limited genetic diversity of farmed fish (Bakke and Harris, 1998; Langevin *et*
74 *al.*, 2012). Although advances in biosecurity and preventative medicine limit the impact of

75 many infectious conditions on marine finfish production (Assefa and Abunna, 2018), other
76 diseases and the influence of uncontrolled environmental variables remain of concern. The
77 presence of gelatinous plankton is just one such environmental variable.

78

79 The study of gelatinous plankton and their impact on fish health has emerged recently as an
80 important field of research. Gelatinous plankton include Ctenophora (commonly known as
81 ‘comb jellies’), salps, and Cnidaria such as the pelagic stages of Hydrozoa and Scyphozoa
82 commonly referred to as ‘jellyfish’. As concern grows regarding the underlying causes of
83 mixed gill pathologies such as proliferative gill disease (PGD) in fish (Król *et al.*, 2020),
84 cnidarian jellyfish in particular are considered of interest regarding their role. Jellyfish are
85 hypothesised to act as waterborne irritants (Downes *et al.*, 2018), initiating or potentiating
86 disease. Jellyfish are also associated with fish mortality events in the aquaculture industry,
87 with reports of loss of thousands of fish across the globe, including in Ireland (Cronin *et al.*,
88 2004), New Zealand (Zaki, 2018) and Tasmania (Ford, 2019). By one estimation, in Scotland
89 between 1999-2005, 2.9 million marine-stage mortalities of Atlantic salmon were attributable
90 to planktonic organisms (Hay and Murray, 2008). Although also implicated in harmful events
91 to fish, Ctenophora are documented less frequently as a challenge to the aquaculture industry
92 (Rodger *et al.*, 2011a). This review therefore provides an overview of the biology and current
93 understanding of the impact of gelatinous plankton on the aquaculture industry, with a focus
94 on cnidarians. The impacts on commercially important marine fish such as Atlantic salmon
95 (*Salmo salar*), sea bream (*Sparus aurata*) and European sea bass (*Dicentrarchus labrax*) are
96 reviewed, with jellyfish species of particular concern to fish health highlighted. Through this
97 review of existing research, current gaps in knowledge are also identified, the study of which
98 might benefit the aquaculture industry directly.

99

100 **2. Cnidarian characteristics**

101

102 **2.1 Jellyfish anatomy, life history and taxonomy**

103

104 The phylum Cnidaria contains the majority of gelatinous coelenterates associated with
105 harmful consequences to aquaculture, including the species commonly described as
106 ‘jellyfish’ (Mills, 1995). Pelagic organisms familiar to beachgoers and marine biologists
107 alike, the stereotypical appearance of a jellyfish is that of an upturned bowl structure with
108 trailing tentacles (Zhang, 2011; Springer and Holley, 2013). There is, however, a great
109 variety of morphology in the Cnidaria within the subphylum Medusozoa that have
110 collectively been described as ‘jellyfish’. This includes Cubozoa, Scyphozoa (‘true’ jellyfish)
111 and Hydrozoa (hydroid jellyfish). Other cnidarian classes such as Polypodiozoa, Myxozoa
112 (endoparasitic organisms) and Anthozoa (corals and anemones) lack a medusoid stage in their
113 life cycles, and are not generally referred to as jellyfish (Springer and Holley, 2013).

114

115 The unique properties of gelatinous plankton have enabled their colonisation of the oceans,
116 with distribution from polar to tropical waters (Lucas *et al.*, 2014). Composed principally of
117 water (95%), collagen and salts, jellyfish are relatively simple organisms, with a limited
118 number of cell types (Johnsen, 2000; Brusca and Brusca, 2003; Larink and Westheide, 2011).
119 Low-cellularity gelatinous mesoglea is metabolically inexpensive to produce, and jellyfish
120 movement expends relatively little energy (Larson, 1987). This appears to be part of the
121 reason they are able to grow as much as twice as fast as other pelagic organisms (Josephson,
122 2004; Neubauer, 2012; Pitt *et al.*, 2013). A varied reproductive repertoire and low energy
123 demand also enable organisms like Cnidaria and Ctenophora to proliferate rapidly in

124 favourable environmental conditions, forming large medusal aggregations known as blooms
125 (Mariottini *et al.*, 2008; Hamner and Dawson, 2009; Pitt and Purcell, 2009).

126

127 The basic life stages of jellyfish include the medusoid free-swimming stages that may form
128 blooms, and benthic polyp stages (Fautin, 2002). Polyps are sessile life stages that grow on
129 various aquatic substrates including underwater aquaculture architecture, such as nets and
130 barges (Guenther *et al.*, 2009; Madin *et al.*, 2009). Polyps do not have the ‘classic’
131 appearance of jellyfish, but this life-stage is nevertheless an important consideration for
132 aquaculture. Polyps can bud asexually to form more polyps, or strobilation occurs for
133 production of ephyrae that grow to become the familiar medusae. Medusae are often bell-
134 shaped with tentacles and may reproduce sexually to create more medusae, or form planulae
135 that settle to form polyps. Optimal conditions and triggers for medusa production are not yet
136 fully understood in the majority of cnidarian jellyfish, but both biotic and abiotic variables
137 drive reproduction and survival, with varied requirements between species (Arai, 1997;
138 Fautin, 2002; Stenseth *et al.*, 2004; Boero *et al.*, 2008). Temperature, salinity and food
139 availability in particular are considered key drivers of bloom events (Purcell *et al.*, 2007;
140 Holst and Jarms, 2010; Purcell, 2012; Lilley *et al.*, 2014).

141

142 Both Cnidaria and Ctenophora coelenterates can negatively impact fish stocks, for example
143 as non-native invasive species and through predatory behaviour impacting food webs (Kideys
144 *et al.*, 2005; Fuentes *et al.*, 2010). Ctenophora, however, differ crucially from Cnidaria in
145 lacking the stinging organelles that make Cnidaria particularly problematic to fish (Springer
146 and Holley, 2013). Cnidarian jellyfish possess specialised cells called cnidocytes that can
147 contain nematocyst stinging organelles, used for capture of prey and defence (Lotan *et al.*,
148 1996; Springer and Holley, 2013). These nematocysts contain a collagenous barb and venom

149 that is extruded, harpoon-like, on discharge of the sting (Beckmann and Özbek, 2012).
150 Although documented primarily on the tentacles and oral arms (Helmholz *et al.*, 2010),
151 nematocysts can be found in all cnidarian epidermal tissue (Springer and Holley, 2013), and
152 are present in both medusoid and polyp life-stages. Discharge of the barb punctures the tissue
153 of prey (Jouiaei *et al.*, 2015), allowing injection of mixed proteinaceous compounds. Species,
154 geographical location and even age of individual Cnidaria impact venom composition
155 (Purcell and Arai, 2001; Radwan *et al.*, 2001; Helmholz *et al.*, 2007, 2010; Mariottini and
156 Pane, 2010).

157

158 Study of venom components of different cnidarians has demonstrated varied constituents
159 such as porins, neurotoxic peptides and bioactive lipids (Purcell, 1984; Nagai *et al.*, 2000).
160 Relatively little is understood about the toxicological effects of cnidarian jellyfish beyond
161 those species of particular concern to public health (Nagai *et al.*, 2000; Kintner *et al.*, 2005;
162 Brinkman and Burnell, 2009; Šuput, 2011; Piontek *et al.*, 2020), or those explored in the field
163 of pharmaceutical discovery (Ovchinnikova *et al.*, 2006). Impact of cnidarian stings are best
164 documented in human medicine, including the immunological and toxinological
165 consequences of envenomation (Tibballs *et al.*, 2011). Some illicit only a mild irritation,
166 while others such as box jellyfish (Cubozoa) can be fatal (Burke, 2002). However, although
167 all Cnidaria possess stings, many of concern to fish health cause no apparent damage in
168 humans, perhaps due to a lack of venom potency in some species, or due to the thick
169 keratinised structure of human skin.

170

171 **2.3 Distribution and reporting of cnidarian jellyfish**

172

173 A great number of variables impact presence of gelatinous plankton. Both cnidarians and
174 ctenophores are successful in nearly every marine environment on earth, as well as some
175 freshwater locations. Some jellyfish species like *Pelagia noctiluca* (the ‘mauve stinger’) and
176 *Aurelia aurita* (‘moon jellyfish’) have wide and even global distributions (Dawson *et al.*,
177 2005; Mariottini *et al.*, 2008). Onshore stranding reports document *A. aurita*, *Chrysaora*
178 *hysoscella* (‘compass jellyfish’), *Cyanea capillata* (‘lion’s mane jellyfish’) and *Cyanea*
179 *lamarckii* (‘blue jellyfish’) as some of the most common Scyphozoa to Scottish waters
180 (Pikesley *et al.*, 2014). Similar species are reported across the coastlines of Norway and
181 Iceland where Atlantic salmon production also occurs. *P. noctiluca*, *Cotylorhiza tuberculata*
182 and *Rhopilema nomadica* are additionally considered common in the Mediterranean where
183 marine farming of gilthead sea bream and sea bass is common (Mariottini and Pane, 2010).
184 Other regions of marine aquaculture production, including Tasmania, Canada and Asian
185 countries such as China, see varied jellyfish species (Dong *et al.*, 2010; Condon *et al.*, 2014).
186 *Chrysaora melanaster*, *C. capillata*, *Staurophora mertensii* as well as *Aequorea* and *Aurelia*
187 species are common in the Northern Pacific, for example (Cieciel and Yasumiishi, 2017),
188 whereas species such as *Chrysaora lactea*, *Aurelia* and *Stomolophus* species are common off
189 the coast of South America (Oliviera *et al.*, 2016; Frolova and Miglietta, 2020) including
190 Chile, where salmonid aquaculture is also an important industry. The majority of existing
191 research is focused on bloom-forming and biofouling jellyfish species of the Northern
192 Atlantic, however that does not mean those of other geographical areas are harmless to fish.
193 Their impact is merely under-explored.

194

195 Data obtained from commercial fisheries, satellites and shoreline surveys provide distribution
196 information towards jellyfish bloom reporting (Fleming *et al.*, 2013). Many scyphozoan
197 species are observable on beaches and at the ocean surface due to their large size and pelagic

198 distribution, but hydromedusae can be difficult to observe due to their small size (Kintner and
199 Brierley, 2018), which means quantitative abundance surveys often fail to record those within
200 the class Hydrozoa (Doyle *et al.*, 2007). Hydromedusa are suggested to be one of the most
201 diverse small gelatinous zooplankton around most coastlines (Russell, 1970; Baxter *et al.*,
202 2012a; Oliviera *et al.*, 2016). However, the majority can only be detected and differentiated
203 reliably by microscopic assessment (Larink and Westheide, 2011), and so population
204 estimates are lacking. Both episodic incursions of oceanic species and locally propagating
205 benthic jellyfish can be observed in near-shore coastal waters (Houghton *et al.*, 2007;
206 Fleming *et al.*, 2013). A growing body of work therefore exists to inform prediction models
207 for jellyfish community fluctuations of both kinds (Goldstein and Steiner, 2019). Factors such
208 as anthropogenic nutrient loading are pertinent to inshore jellyfish communities (Purcell *et*
209 *al.*, 2007; Stoner *et al.*, 2011). Wind direction is considered an important predictor of influx
210 in pelagic species (Gershwin *et al.*, 2014), as are regional atmospheric patterns that influence
211 surface water temperature and precipitation-induced nutrient run-off, such as the North
212 Atlantic Oscillation (NAO) and El Niño (Lynam *et al.*, 2004, 2010; Martin *et al.*, 2006).
213 Species-specific characteristics of jellyfish as drivers of bloom formation also assist in
214 forecasting (Ramondenc *et al.*, 2020). *P. noctiluca*, for example, lacks a sessile benthic life
215 stage, reproducing only by pelagic production of medusae (Larson, 1987; Brusca and Brusca,
216 2003), and therefore represents an influx concern. However, due to a current lack of complete
217 understanding of predictor variables, it is not yet possible to reliably forecast jellyfish
218 population fluctuations that might impact aquaculture.

219
220 Various methods of off-shore population assessment are used to monitor real-time jellyfish
221 populations, including use of Continuous Plankton Recorders (CPR) (Brander *et al.*, 2003), as
222 well as acoustic and optical surveys (Brierley *et al.*, 2005). Methods optimised to address the

223 challenge of assessing microscopic species vary (Xiong *et al.*, 2020), but the most accurate
224 method of sampling these populations remains filtration, collection and taxonomic
225 identification (Harris *et al.*, 2000). Although relatively labour intensive, this monitoring
226 technique is similar to daily cage-side sampling for phytoplankton already performed at many
227 aquaculture sites using simple hand-held apparatus (Arai, 1997). Sampling for jellyfish is not
228 currently routinely performed at the majority of marine aquaculture sites (per comm's,
229 aquaculture producers). This topic was last comprehensively reviewed in 2013, where the
230 authors emphasised the importance of routine population monitoring (Purcell *et al.*, 2013).
231 Seven years on, aquaculture facilities still generally lack any real-time evaluation of
232 environmental jellyfish populations.

233

234 Lack of quantitative historical population data and difficulties in consistent assessments
235 hinder analysis of jellyfish population trends for differentiating oscillations from long-term
236 shifts (Mills, 2001; Purcell, 2005; Sanz-Mart in *et al.*, 2016). Recent surveys track seasonal
237 and annual temporal trends in populations that might be used to inform forecasting, although
238 observing a bloom can be a chance event (Mills, 1991). Although consensus is lacking as to
239 whether jellyfish populations have increased globally in recent history (Purcell, 2005;
240 Condon *et al.*, 2013; Sanz-Mart in *et al.*, 2016), and complex ecological consequences of
241 altered ecosystems and environmental conditions are hard to predict, many studies suggest a
242 beneficial outcome for at least some jellyfish with changing ocean environments. Some
243 populations may decrease or remain stable, but ocean acidification, warming temperatures
244 and altered trophic structures are all predicted to benefit many gelatinous zooplankton (Mills,
245 2001; Richardson and Gibbons, 2008; Richardson *et al.*, 2009; Brotz *et al.*, 2012; Huang *et*
246 *al.*, 2015). Over-fishing is suggested to be a particular driver of shifting abundances for
247 jellyfish dominance. Altered marine conditions can also lead to altered aquatic organism

248 ranges, with the added concern of ingress of non-native species (Ma and Purcell, 2005;
249 Restaino *et al.*, 2018). Overall, evidence suggests bloom events are increasing in the Northern
250 Atlantic ocean, based in-part on increasing detection of gelatinous material in continuous
251 plankton recorder survey's since the early 2000's (Licandro *et al.*, 2010).

252

253 **3. Complex interactions of jellyfish and fish**

254

255 Although often discussed only in terms of the problems they create, it is important to
256 remember that seasonal blooms of Coelenterata play important ecological roles as part of
257 marine food webs and even in carbon sinking (Jaspers *et al.*, 2014; Lebrato *et al.*, 2019).
258 Gelatinous plankton represent an important food source for many marine organisms,
259 including commercially important finfish species (Brodeur, 1990; Osgood *et al.*, 2016).
260 Juvenile fish, sablefish (*Anoplopoma fimbria*) and even chum salmon (*Oncorhynchus keta*),
261 as part of hatchery release aquaculture, all consume jellyfish such as *Chrysaora* (Arai, 1988;
262 Brodeur and Percy, 1992). The myriad interactions between pelagic coelenterates with wild
263 fisheries has been reviewed previously in great detail (Purcell and Arai, 2001), with recent
264 global trends in impact of specific jellyfish on fisheries also available (Bosch-Belmar *et al.*,
265 2020). Competition for prey resources and direct predation on fish larvae and eggs (Purcell,
266 1990; Purcell and Grover, 1990) are just two examples of negative effects on wild stocks.
267 Whilst jellyfish presence can benefit fish species that shelter within swarms, such as juvenile
268 prowlfish (*Zaprora silenus*) and whiting (eg *Merlangius merlangus*), they can also compete
269 directly for resources with commercially important fish such as Pacific herring (*Clupea*
270 *pallasii*) (Lynam *et al.*, 2005; Ruzicka *et al.*, 2020). Recent literature also documents the
271 problem of blooms being caught in nets of fishers, breaking equipment, stinging crew, and
272 even capsizing boats (Kawahara *et al.*, 2006). This jellyfish bycatch is linked with major

273 economic losses through increased fishing effort and reduced catch globally in many fisheries
274 (Purcell *et al.*, 2000; Uye, 2008; Nagata *et al.*, 2009; Dong *et al.*, 2010; Kim *et al.*, 2012;
275 Quiñones *et al.*, 2013; Conley and Sutherland, 2015).

276

277 **4. Jellyfish and aquaculture**

278 The impact of gelatinous plankton in the context of aquaculture is largely negative. This is a
279 global issue, impacting marine finfish aquaculture in Europe, Asia, the Americas and
280 Australia (Clark *et al.*, 1997; Palma *et al.*, 2007; Willcox *et al.*, 2008). Cnidarian jellyfish are
281 considered the most problematic coelenterate, even negatively impacting shellfish
282 aquaculture (Fitridge and Keough, 2013), and freshwater fish (Bose *et al.*, 2019). Many
283 marine species of fish are farmed through aquaculture across the world (**Table 1**), and
284 although the majority of existing research is focused on the impact of Cnidaria on Atlantic
285 salmon and sea bass, much of our existing knowledge may be transferable to other
286 maricultured finfish. The cnidarian species that impact aquaculture are varied, from medusoid
287 scyphozoan species to microscopic hydromedusae and cnidarian polyps. Some of the most
288 extensively studied species are *C. capillata*, *A. aurita* and *P. noctiluca* (**Figure 1**). Limited
289 reports linking Ctenophora to negative consequence in aquaculture are also documented
290 (Purcell and Arai, 2001).

291

292 Biofouling is the growth of unwanted environmental organisms, of which Cnidaria can
293 represent a dominant component. In aquaculture, this growth can occur on structures such as
294 nets and piers. Presence of biofouling organisms such as Cnidaria and algae on nets can
295 reduce water flow, allowing accumulation of suspended solids and resulting in reduced
296 dissolved oxygen concentration, both parameters known to cause subsequent impairments of
297 fish health (Nyanti *et al.*, 2018; Cornejo *et al.*, 2020). In addition to this indirect impact on

298 fish through alteration of environmental conditions, cnidarian biofouling organisms can also
299 directly harm fish through their stinging mechanisms (Bloecher *et al.*, 2018). Previous
300 literature reviews provide in depth description of the challenges associated with biofouling
301 (Fitridge *et al.*, 2012). In summary though, cnidarians of concern in biofouling include
302 species within the *Ectopleura*, *Obelia*, *Pennaria*, *Plumularia* and *Tubularia* genera, with
303 recorded growth in a range of aquaculture industries, from Norwegian Atlantic salmon to
304 Malaysian Barramundi (*Lates calcarifer*) production (Madin *et al.*, 2009; Guenther *et al.*,
305 2011; Bosch-Belmar *et al.*, 2017a). A concern discussed in detail below ('Consequences of
306 jellyfish exposure to fish health') is that the negative feedback of increased substrate such as
307 nets and docks with increased aquaculture may be further amplifying the problem of both
308 benthic Cnidaria and associated pelagic medusae through biofouling.

309

310 The cnidarian classes Polypodiozoa and Myxosporea are also of note with regards to their
311 negative impact on fish health, although they are not considered jellyfish. Parasites of both
312 farmed and wild finfish, infections can be particularly devastating within the high-density
313 confines of aquaculture (Rigos *et al.*, 1999; Jones *et al.*, 2015; Groner *et al.*, 2016). Beyond
314 the scope of this review, parasitic cnidarian infections of fish are reviewed elsewhere
315 (Garden, 1992; Yokoyama, 2003; Mackenzie and Kalavati, 2014). Briefly though, Myxozoa
316 are parasites that can infect various organs of fish in both marine and freshwater
317 environments (Feist and Longshaw, 2006) (**Figure 2**). Only recently taxonomically classified
318 (Atkinson *et al.*, 2018), much is still to be learned about these abstruse organisms (Mackenzie
319 and Kalavati, 2014). Some examples associated with impaired production in important
320 aquaculture species include *Myxobolus cerebralis*, causative agent of 'Whirling disease'
321 (Ryce *et al.*, 2005), and *Tetracapsuloides bryosalmonae*, the causative agent of Proliferative
322 Kidney Disease (PKD) (Canning *et al.*, 2002), in salmonids. *Henneguya ictaluri* in catfish

323 and *Parvicapsula pseudobranciola* in salmonids impact North American aquaculture
324 (Karlsbakk *et al.*, 2002; Gomes *et al.*, 2014). *Myxobolus holzeriae* infection is associated with
325 high mortality in cyprinids (Gupta and Kaur, 2017), whereas *Enteromyxum* species are
326 considered particularly pathogenic in sea bream (Diamant *et al.*, 1994; Gomes *et al.*, 2014).
327 *Kudoa* species infections cause myoliquefaction of muscle and therefore reduction of quality
328 of fillets, as well as being a public health concern for human allergy sufferers (Moran *et al.*,
329 1999; Kristmundsson and Freeman, 2014). *Polypodium hydriforme*, a parasite of fish eggs, is
330 the only documented living representative of the monotypic Polypodiozoa class (Evans *et al.*,
331 2008). Overall, parasitic Cnidaria result in impaired fish health throughout the global finfish
332 industry, with reduced production and increased mortalities as well as post-harvest discards
333 due to their direct infective impact (Kent *et al.*, 1994).

334
335 The cnidarians most commonly referred to as jellyfish (Scyphozoa and Hydromedusae) are
336 problematic to aquaculture in a different way. Frequently described as ‘pests’, this moniker
337 falls some way short of illustrating the impact of these organisms on farmed fish. The
338 association of jellyfish blooms with mass mortalities in farmed fish has been documented
339 over a number of decades in a variety of finfish aquaculture sectors, including entire farm
340 fish-kills with loss of millions of dollars-worth of stock (Bruno and Ellis, 1985; Seaton, 1989;
341 Doyle *et al.*, 2008; Nickell *et al.*, 2010). Species implicated in these large-scale mortality
342 events of farmed fish around the world include medusal *A. aurita*, *P. noctiluca*, *Phialella*
343 *quadrata* and *Solmarisidae* species (Bruno and Ellis, 1985; Mitchell *et al.*, 2011b; Raffaele,
344 2013; Munro, 2014; Bosch-Belmar *et al.*, 2016a, 2017b; Forseth *et al.*, 2017). Recent
345 research now seeks to explore the mechanisms of this harm, including sub-lethal exposure
346 and the potential involvement of jellyfish in insidious stock loss, as well as important
347 production diseases.

348

349 Jellyfish of concern to aquaculture can come into contact with fish in a number of ways.

350 Free-swimming Hydrozoa and some Scyphozoa are small enough to pass through the nets of

351 sea cages and be inhaled or ingested by fish (Mitchell *et al.*, 2011b), passing over epithelial

352 tissue of the gills and through the gastrointestinal tract (GIT) (Powell *et al.*, 2018). Larger

353 Scyphozoa like *C. capillata* and *A. aurita* are easily damaged in strong currents or when

354 pushed against nets in bad weather, so pieces of tissue of these organisms can also pass

355 through nets to contact fish (Baxter *et al.*, 2011a, 2011b; Rodger *et al.*, 2011a) (**Figure 3**).

356 Sessile polyp life stages not only negatively impact marine cage hygiene, they are also

357 associated with traumatic damage to fish: Seasonal budding and power-washing employed by

358 inshore Atlantic salmon producers to clean fouled nets causes dispersal throughout the water

359 column, leading to damage of the fish (Hodson *et al.*, 1997; Guenther *et al.*, 2010; Baxter *et*

360 *al.*, 2012b; Fitridge *et al.*, 2012). This phenomenon is recognised in varied aquaculture

361 production industries, particularly with respect to the hydroid *Ectopleura larynx* (Guenther *et*

362 *al.*, 2010; Baxter *et al.*, 2012b; Bosch-Belmar *et al.*, 2017a). Infrastructure such as net pens

363 increase substrate for the benthic polyp life stages, potentially amplifying the issue further

364 (Duarte *et al.*, 2013). Species of concern are summarised in **Table 2**.

365

366 **5. Consequences of jellyfish exposure to fish health**

367

368 Recent research sheds light on the mechanisms of fish kills from jellyfish, as well as sub-

369 lethal consequences of exposure in cultured fish (Doyle *et al.*, 2007; Kintner and Brierley,

370 2018). There are currently three suggested processes of negative impact; direct traumatic

371 damage to tissue, in initiation of secondary disease, and through physiological compromise,

372 either by direct occlusion of the gill surface, or altered gill function.

373

374 **5.1 Physical tissue damage**

375

376 All Cnidaria possess cnidocytes, and it is the action of this stinging mechanism that results in
377 fish trauma, through a combination of barb extrusion and venom exposure (Bruno *et al.*,
378 2013). Cnidarian venoms have been demonstrated as toxic to fish epithelial cultures and
379 tissue (Mariottini *et al.*, 2002; Helmholz *et al.*, 2010), causing haemolysis and cytotoxicity. *In*
380 *vivo* exposure of fish has demonstrated jellyfish-induced damage to skin, gills, and
381 gastrointestinal tissues (**Figure 4**). Histological assessment demonstrates the damage appears
382 particularly pronounced in gill tissue, documented in both naturally occurring and controlled
383 exposure of Atlantic salmon, European sea bass and sea bream. A number of marine jellyfish
384 including *A. aurita* (Baxter *et al.*, 2011b; Mitchell *et al.*, 2011b), *C. capillata* (Powell *et al.*,
385 2018) and *P. noctiluca* (Mitchell *et al.*, 2012; Marcos-Lopez *et al.*, 2014; Bosch-Belmar *et*
386 *al.*, 2016a) have been shown to induce histopathological changes in tissues. Although
387 individual venom components differ between species (Helmholz *et al.*, 2007, 2010;
388 Mariottini *et al.*, 2008; Ponce *et al.*, 2013), the reported histological impact upon fish gills is
389 similar. Acute damage presents as multifocal tissue changes with haemorrhage, epithelial
390 necrosis and sloughing. This is accompanied by reported erythrocyte lysis, and progresses to
391 a granulomatous immune response with oedema (**Figure 2**). Similar to many other gill
392 disorders, reported progressive pathology includes lamellar fusion and hyperplastic change
393 (Baxter *et al.*, 2011b; Mitchell *et al.*, 2011a; Powell *et al.*, 2018), with resolution within
394 approximately a month. Skin lesions are characterised by an acute dermatitis of
395 predominantly neutrophilic cells. Haemorrhage, oedema and epithelial necrosis are also
396 described in the skin. The severity of pathological change is positively correlated with
397 exposure intensity, with protracted healing reported following greater exposure levels.

398

399 In addition to the above scyphozoan species, many other Cnidaria have also been linked to
400 pathology in marine fish. Gill disease has been reported in farmed fish following high-density
401 environmental exposure to many hydrozoan species, including *P. quadrata*, *Solmaris corona*,
402 *Lizzia blondina*, *E. larynx*, *Muggiaea atlantica*, and *Apolemia uvaria*, as well as additional
403 *Solmarisidae* and *Obelia* species (Bamstedt *et al.*, 1998; Helmholz *et al.*, 2010; Baxter *et al.*,
404 2011a, 2012b; Mitchell *et al.*, 2011b; Munro, 2014; Kintner and Brierley, 2018; Powell *et al.*,
405 2018). Further research suggests the involvement of additional species in fish mortality or
406 other altered health events, including *Catablema vesicarium*, *Dipleurosoma typicum* and
407 *Verella verella* (the ‘by the wind sailor’ jellyfish) (Purcell *et al.*, 2007; Rodger *et al.*, 2011b;
408 Halsband *et al.*, 2018). These hydrozoan jellyfish species, many of which cannot be detected
409 with the naked eye and yet represent the bulk of medusal diversity in the marine environment,
410 appear factors in increased gill pathologies and salmonid mortalities. *S. corona* is particularly
411 lethal; the hydromedusae of this jellyfish have been implicated in large-scale mortality events
412 in Atlantic salmon (Bamstedt *et al.*, 1998). Other microscopic species are suggested to elicit
413 more chronic disease in fish (Baxter *et al.*, 2011a), raising interesting research questions as to
414 their involvement in mixed or unexplained gill pathologies of farmed fish.

415

416 The delicate lamellae of gills, reported location of trauma of many Cnidaria, lack the
417 protective, stratified layers of human epithelium (Roberts, 2012; Jenkins and Tortora, 2013),
418 and the scales of fish skin. Gastric lesions following jellyfish exposure through the proposed
419 mechanism of ingestion of cnidarian tissue are also reported in fish (Rodger *et al.*, 2011b),
420 and present an interesting question as to the eating habits of fishes that deliberately ingest
421 jellyfish. Partially digested gelatinous material is morphologically indistinct and appears to
422 breakdown rapidly within the stomach of fish, so limited information is available regarding

423 any species-specific feeding habits, but discriminate feeding might protect fish that feed
424 specifically on jellyfish. DNA-based sequencing analysis of stomach contents is now
425 shedding light in this topic (Sakaguchi *et al.*, 2017).

426

427 **5.2 Physiological consequences of exposure**

428

429 Disruption of epithelial tissue in contact with the aquatic environment in fish is frequently
430 accompanied by a loss of functional ability (Stoskopf, 1993). Gills perform a number of
431 essential roles in fish survival, including respiration, osmoregulation and defence. Similar to
432 other environmental stressors, and suggested by the clear traumatic outcomes of exposure,
433 jellyfish exposure in fish likely results in a stress response within fish tissue. Behavioural
434 changes suggest an impaired uptake of oxygen in addition to epithelial irritation (Baxter *et*
435 *al.*, 2011b; Powell *et al.*, 2018), with subsequent changes indicating the potential for
436 complete loss of equilibrium, resulting in death. Inflammatory changes observed through
437 histopathology indicate an immunological response within tissue in response to jellyfish-
438 induced trauma (Rodger *et al.*, 2011b; Powell *et al.*, 2018). There currently exists no research
439 on altered gene expression of any fish following exposure of any jellyfish species, and so no
440 information regarding molecular-level fish responses to jellyfish exposure, although existing
441 research has explored the host response to myxozoan infections (Sudhagar *et al.*, 2019).
442 Jellyfish studies have, however, measured antioxidant enzyme production and increased
443 polysaccharide (mucus) secretion by sea bream in response to *P. noctiluca* (Ensibi *et al.*,
444 2017) as part of sub-lethal exposure (Lovy *et al.*, 2007; Marcos-López *et al.*, 2018).
445
446 Physiological consequences of jellyfish exposure in fish include altered oxygen uptake, and
447 altered blood biochemistry parameters. Assessment of blood biochemistry following *C.*

448 *capillata* exposure in Atlantic salmon indicates altered gill function with reduced carbon
449 dioxide excretion, alongside increased sodium and potassium levels (Powell *et al.*, 2018).
450 These changes, considered alongside an increased haematocrit, are consistent with a stress
451 response in fish, as well as suggestive of altered osmoregulatory ability. *P. noctiluca*
452 envenomation similarly alters critical ambient oxygen tension requirements (PO_{2crit}) and
453 oxygen uptake in European seabass, resulting in enhanced sensitivity to hypoxia (Bosch-
454 Belmar *et al.*, 2016b). Altered gill structure, with reduction in functional gill surface area for
455 oxygen uptake, could reasonably explain altered respiratory effort in fish. Previous
456 publications have also suggested an action in altered oxygen availability with jellyfish
457 blooms, both through direct occlusion of the gill surface by the gelatinous bodies of jellyfish
458 and by aggregation of jellyfish around net margins preventing water exchange (Mitchell *et*
459 *al.*, 2011b). There exists a single report of the ctenophore *Bolinopsis infundibulum* acting in
460 this way, directly suffocating fish in Norway (Bamstedt *et al.*, 1998). Altered respiratory
461 function might therefore be induced by a combination of direct occlusion and impaired gill
462 function from tissue damage by cnidarians. Any alteration of osmoregulatory function
463 through trauma might also occur in combination with toxic effects of venom, such as the
464 neurotoxic sodium channel-blocking effects of *C. capillata* venom (Lassen *et al.*, 2012;
465 Powell *et al.*, 2018). Mammalian exposure studies also demonstrate the action of *A. aurita*
466 and *C. capillata* venom in membrane disruption of cells (Helmholz *et al.*, 2010). Although
467 altered biochemical parameters or haematocrit values are not diagnostic for specific diseases
468 due to their varied functions and physiological pathways of change, alterations in these
469 parameters do clearly indicate an altered homeostasis with compensatory mechanisms in fish
470 with jellyfish exposure.

471

472 **5.3 Secondary infections following exposure**

473

474 A commonly reported secondary sequelae of jellyfish exposure and frequent feature of
475 subsequent gill pathology is bacterial disease (Mitchell *et al.*, 2011b; Bosch-Belmar *et al.*,
476 2017a). Many infections likely represent opportunistic, environmental colonisation (Belkin
477 and Colwell, 2005). A small body of research, however, suggests that jellyfish themselves
478 might act as vectors of infectious disease (Ferguson *et al.*, 2010; Delannoy *et al.*, 2011). Like
479 all aquatic organisms, Cnidaria host a distinct and apparently specialised microbiota on their
480 tissue surfaces (Manzari *et al.*, 2014; Weiland-Brauer *et al.*, 2015; Brown *et al.*, 2017).
481 Bacteria associated with infectious disease in fish have been identified within the microbiota
482 of a number of jellyfish considered harmful to aquaculture (Schuett and Doepke, 2010;
483 Clinton *et al.*, 2020). The direct action of vector-mediated introduction might then also occur,
484 with the suggested analogy of a ‘dirty needle’ delivery of microbiota by stinging cnidocytes.
485 *P. noctiluca* is associated with tenacibaculosis outbreaks in Atlantic salmon (Småge *et al.*,
486 2017), with suspected transfer of the causative agent *Tenacibaculum maritimum* between fish
487 and jellyfish (Ferguson *et al.*, 2010; Delannoy *et al.*, 2011). Both Cnidaria and Ctenophora
488 are also documented hosts of parasitic pathogens, including trematodes and nematodes
489 (Svendsen, 1990; Martorelli, 1996, 2001), but natural transmission to fish is reported to be
490 low (Marcogliese, 1995).

491

492 Due to their delicate structure and lack of protective scales, gills are the site of entry of many
493 pathogens. An important function of gills is therefore in defence. One key element of this is
494 production of immunologically active mucus (Lumsden *et al.*, 1994; Koppang *et al.*, 2015), a
495 product that can exclude harmful agents from the surface of gills. Mucus also aids in
496 osmoregulation in the marine environment, although excessive production will compromise
497 respiratory efficiency (Handy *et al.*, 1989; Evans *et al.*, 2005). An immune response to

498 jellyfish challenge in fish is suggested by the inflammatory infiltrate noted in histopathology
499 of traumatised gills, and expected as part of a stress response. An altered immune status
500 might also partially explain the apparent predisposition of fish to subsequent infectious
501 pathologies. Although no link was found with amoebic gill disease infection rate (AGD) and
502 biofouling exposure (Bloecher *et al.*, 2018), many studies report secondary pathologies
503 following jellyfish exposure as a factor in subsequent fish deaths (Marcos-Lopez *et al.*,
504 2014). Therefore, a credible hypothesis is for the involvement of jellyfish as mild to moderate
505 gill irritants, impairing healthy gill function, and predisposing to subsequent disease through
506 altered tissue structure, function and stress tolerance (Marcos-Lopez *et al.*, 2014; Clinton *et*
507 *al.*, 2020).

508

509 An understanding of the transcriptomic and proteomic consequences of jellyfish exposure in
510 fish will be key to truly understand the mechanisms of their impact, and potential
511 involvement in other pathologies. The varied properties of venom, direct cellular damage and
512 resultant physiological compromise might all be reflected in altered patterns of fish response.
513 Also, multifactorial gill diseases are a common complaint particularly in farmed Atlantic
514 salmon, with important commercial and welfare ramifications. A complex and as yet not fully
515 understood suite of environmental and infectious factors appear to influence the development
516 of mixed gill infections in these fish, of which jellyfish as gill irritants might be key.
517 However, due to a current lack of surveillance of cnidarian populations, demonstration of
518 cause and effect in these pathologies is problematic. Association of jellyfish with initiation or
519 potentiation of disease in aquaculture, as part of their tissue disruptive or immunological
520 consequences, represents then a key area for future research in the field of gill health.

521

522 **6. Surveillance and mitigation**

523

524 Although an area with less routine disease surveillance (Jeffries *et al.*, 2014), wild fisheries
525 do not appear to suffer from a jellyfish problem of equal magnitude to that found in
526 aquaculture. This may be due to a number of factors, including the genetic and
527 immunological status of farmed fish. High stocking density of the caged environment and the
528 inability of fish to escape from water-borne irritants and insults are likely to be important
529 factors. The full economic impact of jellyfish on aquaculture is, however, hard to quantify at
530 present. Sporadic mass mortality events have a clear financial cost to aquaculture, with
531 economic losses due to jellyfish in fisheries estimated in their millions (Palmieri *et al.*, 2014).
532 The involvement of jellyfish in gill pathologies is currently unquantifiable, but gill disease is
533 considered one of the most economically significant challenges to Atlantic salmon production
534 (Mitchell *et al.*, 2011a) and so the financial cost of jellyfish may be very high.

535

536 Key to informing mitigation strategies and understanding the full economic burden of
537 jellyfish is an understanding of harmful species and population exposure densities, for which
538 various metrics are available. Available data regarding density and consequences of exposure
539 are summarised in **Table 2** for jellyfish species linked to negative effects in aquaculture. It is
540 noteworthy that size variation in species such as *C. capillata* and *A. aurita* likely impact
541 exposure intensity, due to a combination of factors such as nematocyst density and venom
542 components (Colin and Costello, 2007). *P. noctiluca* is a relatively small jellyfish for which
543 exposure as low as 10 individuals / m³ (1.2 g/L) has been demonstrated to induce gill
544 pathology in gilthead sea bream (Bosch-Belmar *et al.*, 2016a). *C. capillata* exposure at 2.5
545 g/L has been shown to induce similar behavioural, physiological and histological changes
546 through experimental challenge (Powell *et al.*, 2018). Publications measuring environmental
547 populations tend to do so by extrapolating total individuals from sampling efforts, a technique

548 well suited to hydromedusae communities of more uniform size. Environmental challenge
549 also presents a more complicated picture of exposure through the presence of mixed planktic
550 communities. Experiments simulating net-washing observe gill pathology attributed to *E.*
551 *larynx* exposure (Baxter *et al.*, 2012b), including at concentrations below environmental
552 concentrations suggested to be experienced by fish during net-washing of high-density
553 biofouling (Bloecher *et al.*, 2018). Although individual fish outcomes likely vary with size
554 and health status of fish, overall exposure trials have provided important initial population
555 density data towards understanding cnidarian impacts and protecting aquaculture. Current
556 within-company guidelines of different aquaculture companies make varied
557 recommendations as to the frequency of net washing that should be performed to prevent
558 build-up of biofouling organisms, with some performing twice-monthly washes to remove
559 fouling organisms (Bloecher *et al.*, 2015). Through use of the results of these studies an
560 optimised cleaning threshold might be established, to keep nets clean but minimise harm to
561 fish (Floerl *et al.*, 2016). There are also likely to be unexplored problematic species for which
562 exposure densities of concern must be determined (Mitchell *et al.*, 2012).

563

564 An accurate picture of jellyfish populations in the inshore coastal environments where
565 aquaculture is performed is currently lacking. But jellyfish present a challenge in their
566 identification in real-time, due in part to their changeable body configuration during
567 movement and translucent appearance. Unlike chlorophyll containing phytoplankton,
568 gelatinous zooplankton are not as easily visualised using satellite imaging (Johnsen and
569 Widder, 1998, 1999). Although large aggregations of macroscopically visible species within
570 the upper water column can be seen using satellite imaging, and recent innovations in
571 remotely operated aerial surveillance have been utilised to identify blooms (Schaub *et al.*,
572 2018), both these techniques fail to capture taxonomic diversity, particularly of microscopic

573 species. They do have merit though as part of early warning systems for offshore jellyfish
574 blooms. Traditional computer-aided vision techniques utilising cameras also allow detection,
575 but rarely species differentiation (Rife and Rock, 2003). Sonar applications in real-time
576 monitoring with machine learning are a recent suggested solution (Martin-Abadal *et al.*,
577 2020), however, few publications exist on this topic, and the methods are yet to be
578 demonstrated as practical for monitoring of microscopic species in fish farms. A method that
579 allows assessment of microscopic species abundance is key. Use of novel eDNA technology
580 represents an exciting avenue of monitoring in this context, although it is currently limited in
581 scope by a lack of available environmental data for population density validation. Predictive
582 models may also be of great benefit to aquaculture, so instead of reacting to blooms,
583 producers might take pre-emptive steps in mitigation (Elzeir *et al.*, 2005). Predictive models
584 are already being employed with some success to provide early warning for jellyfish of
585 concern to human health (Gershwin *et al.*, 2014), and as the scientific community's
586 understanding of the variables that precede bloom events are further elucidated, models will
587 become more accurate. As it is, these models still require ground truthing with data regarding
588 exposure outcomes in fish. Long-term population assessment datasets will inform distinctions
589 between routine environmental densities and harmful bloom densities. This information,
590 considered alongside fish health data, will assist in elucidating the full involvement of
591 jellyfish in mixed gill pathologies. Simple-to-perform cage-side zooplankton trawls and
592 accurate data recording at farm sites would easily address this knowledge gap. Detailed
593 guidelines are already available, published by the Scottish Association for Marine Science
594 (Fox and Beveridge, 2013).

595

596 Once exposure levels of jellyfish are understood and real-time monitoring implemented,
597 population densities that should cause alarm might be characterised, and mitigation strategies

598 employed. In the context of sessile life-stages, routine net cleaning has been shown to reduce
599 biofilm build up, keeping exposure levels low. Removal of polyps by divers, mechanically or
600 even through biological control (Berryman, 1984) also goes some way to reducing the
601 problem of water-column distribution associated with power-washing. Coated nets are
602 another strategy available to producers, to reduce initial settlement and build-up of fouling
603 organisms (Guenther *et al.*, 2011). Mitigation of medusal impact might then be achieved
604 solely by reduction of benthic populations that produce them. Protection from advected
605 blooms, however, must involve exclusion from the cage environment, or at least reduction of
606 their impact (Lucas *et al.*, 2012). Success has been reported with short-term tarpaulin use
607 around marine cages for jellyfish exclusion, and screens, wave generators, or nets such as are
608 used to exclude jellyfish from swimming beaches might also be employed to protect farms.
609 Jellyfish exclusion nets are already available for the purpose of reducing exposure of stock to
610 blooms (Piraino *et al.*, 2016), although it is unknown if this will reduce water flow similar to
611 shielding methods used in sea lice exclusion (Frank *et al.*, 2014). These methods are also
612 largely focused on exclusion of macroscopic jellyfish, and fail to address the problem of
613 microscopic species.

614

615 Mitigating strategies might include increasing water oxygenation to optimise respiratory
616 uptake and reduce fish stress. Suspension of feeding or otherwise discouraging surface
617 swimming of fish displaces them lower in the water column, away from surface planktonic
618 food sources that attract jellyfish populations (Purcell *et al.*, 2013; Wright *et al.*, 2017). An
619 additional proposed strategy, although not always practical, includes moving sea cages during
620 a bloom event. These techniques have been suggested for reduced impact of other planktic
621 organisms, but largely remain to be explored in the context of jellyfish. Use of bubble nets
622 has, however, seen some success in exclusion of mixed jellyfish populations. Although they

623 are logistically problematic to implement around net-pens (Lo, 1991), bubble nets have been
624 demonstrated as highly effective under certain conditions (Haberlin *et al.*, 2021), and so with
625 further work bubble nets might present an effective exclusion strategy in at least some
626 instances.

627

628 In addition, farm location is an important risk factor in exposure to blooms, as it is for many
629 pathogenic agents borne by prevailing tides (Graham *et al.*, 2001). Off-shore sites benefit
630 from high-energy water movement. Inshore tidal sites with poor emptying (such as narrow
631 entry sea lochs) are reported to suffer prolonged exposure when a bloom influx occurs and is
632 not drawn out by the tide (per comm's, aquaculture producers). Near-shore farms are also
633 more likely located in the environment of locally propagating blooms (Nickell *et al.*, 2010).
634 More research is required before aquaculture production can be linked directly with increased
635 bloom incidence, however, it does alter local environmental conditions in a predictable
636 manner and provide additional substrate that suggests polyp growth will be favoured (Islam,
637 2005; Makabe *et al.*, 2014). Although there currently exists no 'best' method of jellyfish
638 exclusion or reduction of impact in marine cages, a number of mitigation strategies described
639 above for exclusion and impact reduction may be helpful. Due to the challenge of excluding
640 any organism in the marine environment, future research might consider exploring genomic
641 solutions to the jellyfish problem, such as selective breeding or even vaccination. Exploration
642 of the transcriptomic response to jellyfish exposure seems a logical first step in exploring this
643 potential. Methods of exploiting this response for protection from jellyfish, either through
644 genetic selection or even preventative medicine, might then become apparent. However, this
645 research is, for now, some way off.

646

647 **7. Future Directions**

648
649 Cnidaria are present at a near ubiquitous level in the marine environment as well as
650 freshwater systems, and are a diverse phylum that can impact fish health in a number of
651 ways. This review focuses on the negative consequences to aquaculture from the sessile
652 biofouling and the medusoid cnidarian stages commonly referred to as jellyfish. A number of
653 large-scale fish mortality events of high economic consequence to the aquaculture industry
654 have raised awareness of this challenge to finfish production in recent years. The full
655 economic impact of jellyfish specifically on marine aquaculture is however not yet fully
656 understood, and likely under-reported. Production costs vary (Iversen *et al.*, 2020), but
657 financial investment in fish is cumulative until harvest, meaning potential producer losses in
658 the thousands, not only from mortalities, but also any involvement in reduced growth,
659 impaired production, or necessitated early harvests. Research is yet to explore any specificity
660 of jellyfish harm to individual fish species, although it seems reasonable that jellyfish such as
661 *P. noctiluca* and *C. capillata* have the potential to impact varied aquaculture operations. A
662 warming climate, changing population dynamics of marine food-webs and increasing reports
663 of jellyfish in and around aquaculture facilities also suggests the prospect of increasing bloom
664 events. Increased bloom incidence is predicted for key species of concern to aquaculture
665 (Lynam, Lilley *et al.*, 2011). *P. noctiluca*, for example, is predicted to increase in abundance
666 throughout its range, which includes areas of importance to marine aquaculture such as the
667 North East Atlantic, Mediterranean, and the coasts of Australia and Tasmania (Goy *et al.*,
668 1989; Purcell *et al.*, 1999; Doyle *et al.*, 2008). Factors introduced by aquaculture might also
669 mean increased jellyfish populations (Hamner and Dawson, 2009; Bosch-Belmar *et al.*,
670 2019).
671

672 With the potential for increasing jellyfish exposure, an understanding of the impact of
673 jellyfish and the negative consequences in fish is more important than ever to safeguard the
674 health of stock. A number of studies have clearly demonstrated the negative consequences to
675 fish health of even microscopic cnidarian exposure. Tissue pathology, physiological
676 consequences and secondary infectious pathologies all appear important outcomes in
677 connection with jellyfish. Further health consequences of exposure remain to be explored,
678 including the influence of jellyfish-associated trauma as part of mixed gill pathologies. Gill
679 pathologies of unknown or complex aetiology are a topic of importance to Atlantic salmon
680 production in particular, impacting welfare and survival. Hydrozoa and Scyphozoa are
681 hypothesised to act as environmental irritants, with altered tissue defences and function
682 resulting from jellyfish exposure suggested to predispose fish to infectious pathologies
683 (Martorelli, 2001; Ferguson *et al.*, 2010; Delannoy *et al.*, 2011). However, a lack of routine
684 monitoring for jellyfish means they can go undetected when present. Existing literature
685 demonstrates clearly that jellyfish-induced trauma can be protracted in terms of tissue
686 changes, and so sub-clinical pathologies or subtle impairment of production as a result of
687 jellyfish exposure might often go unreported. Without real-time jellyfish data, it is
688 problematic to retroactively link these organisms to subsequently identified changes in fish
689 health or production indices, and so the full negative impact of Cnidaria on aquaculture
690 remains unexplored.

691

692 Characterising acceptable versus harmful densities of exposure will be key to informing
693 future mitigation strategies. Existing research represents an exciting first step towards the
694 development of guidelines for industry. However, despite the important progress made in the
695 study of cnidarian impact on fish health in the laboratory, lack of routine monitoring of
696 jellyfish populations still impedes the study of the risks posed by cnidarian jellyfish to

697 aquaculture. Monitoring of environmental jellyfish community composition and densities
698 alongside fish health surveillance will provide data for understanding the role of jellyfish in
699 predisposing and potentiating clinical disease in fish. Jellyfish coastal population structure
700 must be correlated with tracked fish health indices, such as gill health, or blood biochemistry.
701 Defined problematic densities will then inform forecasting models and mitigation strategies.
702 Collating such data will also inform advances in monitoring, such as the use of eDNA for
703 detection of specific organisms, by providing validated data of taxa present and exposure
704 densities.

705

706 Many scientists predict that, barring global impetus for change, the marine environment of
707 the future will host drastically altered marine food webs and species diversity from those we
708 see today (Jackson, 2009). Fisheries depletion, habitat destruction, eutrophication and ocean
709 warming with increased acidification might all enhance a shift in species composition
710 towards dominance of gelatinous plankton in coastal and pelagic ecosystems. This shift will
711 put increased stress on human activities in the oceans (Richardson *et al.*, 2009). With
712 increasing global reliance on aquaculture to meet demand for marine fish harvest (Troell *et*
713 *al.*, 2014; FAO, 2020), the health and welfare of farmed fish must be safeguarded. Research
714 has moved forward particularly in the fields of prevention of infectious disease, but the
715 protection of fish from non-infectious organisms remains problematic. Better understanding
716 of the negative impacts of cnidarians upon fish will be key for informing adaptation of the
717 industry, as shifting populations of jellyfish in warming seas look set to affect the aquaculture
718 industry with increasing frequency.

719

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731

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733 This review is the product of the PhD thesis of MC following completion of research
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1377 **Figure 1: Geographical distribution of jellyfish species of concern to aquaculture**
1378 **production**

1379 Map illustrates the global distribution of three well studied species of cnidarian jellyfish,
1380 reviewed as amongst the most problematic to aquaculture production (Bosch-Belmar *et al.*,
1381 2020). Map was generated using open access datasets from OBIS (pre 1900's - 2017) (OBIS,
1382 2020) using statistical software R and package 'rworldmap' (South, 2011). Species data is
1383 differentiated by colour; *A. aurita* (pink), *C. capillata* (yellow) and *P. noctiluca* (blue).

1384

1385 **Table 1: Top marine finfish aquaculture producers globally**

1386 Table lists the top producers of marine finfish (by tonnes) (FAO, 2015). Freshwater
1387 production is not included. Although methods of production vary across maricultured species,
1388 many of these fish are reared in marine sea cages, and therefore potentially vulnerable to
1389 regional jellyfish.

1390

Country	Tonnes produced (% global finfish mariculture)	Finfish mariculture species
Norway	1 245 399 (21.6%)	Atlantic salmon (<i>Salmo salar</i>)
		Rainbow trout (<i>Oncorhynchus mykiss</i>)

		Atlantic cod (<i>Gadus morhua</i>)
		Atlantic halibut (<i>Hippoglossus hippoglossus</i>)
		Spotted wolffish (<i>Anarhichas minor</i>)
		Char (<i>Salvelinus alpinus</i>)
China	1 123 576 (19.4%)	Common seabream (<i>Pagrus pagrus</i>)
		Blackhead seabream (<i>Acanthopagrus schlegelii</i>)
		Groupers
		Cobia (<i>Rachycentron canadum</i>)
		Greater amberjack (<i>Seriola dumerili</i>)
Chile	736 310 (12.7%)	Atlantic salmon (<i>Salmo salar</i>)
		Rainbow trout (<i>Oncorhynchus mykiss</i>)
		Chinook salmon (<i>Oncorhynchus tshawytscha</i>)
		Coho salmon (<i>Oncorhynchus kisutch</i>)
Indonesia	720 545 (12.5%)	Milkfish (<i>Chanos chanos</i>)
		Grey mullet (<i>Mugil cephalus</i>)
		Asian seabass (<i>Lates calcarifer</i>)

		Groupers
		Other seabass
		Cobia (<i>Rachycentron canadum</i>)
		Pompano (<i>Trachinotus blochii</i>)
Philippines	375 735 (6.5%)	Milkfish (<i>Chanos chanos</i>)
		Mixed seabass
		Cobia (<i>Rachycentron canadum</i>)
Japan	242 905 (4.2%)	Japanese amberjack (<i>Seriola quinquerediata</i>)
		Red seabream (<i>Pagrus major</i>)
		Coho salmon (<i>Oncorhynchus kisutch</i>)
		Olive flounder (<i>Paralichthys olivaceus</i>)
		Japanese jack mackerel (<i>Trachurus japonicus</i>)
		Greater amberjack (<i>Seriola dumerili</i>)
United Kingdom	156 220 (2.7%)	Atlantic salmon (<i>Salmo salar</i>)
		Rainbow trout (<i>Oncorhynchus mykiss</i>)
		Atlantic halibut (<i>Hippoglossus hippoglossus</i>)

Greece	124 740 (2.2%)	Gilthead seabream (<i>Sparus aurata</i>)
		European seabass (<i>Dicentrarchus labrax</i>)
		Bluefin tuna (<i>Thunnus thynnus</i>)
Canada	122 024 (2.1%)	Atlantic salmon (<i>Salmo salar</i>)
		Chinook salmon (<i>Oncorhynchus tshawytscha</i>)
		Rainbow trout (<i>Oncorhynchus mykiss</i>)
		Arctic char (<i>Salvelinus alpinus</i>)
Turkey	110 845 (1.9%)	European seabass (<i>Dicentrarchus labrax</i>)
		Gilthead seabream (<i>Sparus aurata</i>)
		Bluefin tuna (<i>Thunnus thynnus</i>)

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1393 **Figure 2 Histological sections of cnidarian impact in fish tissues.**

1394 A. *Tetracapsuloides bryosalmonae* (causative agent of PKD) in H&E stained salmonid

1395 kidney tissue section (x400 magnification). Parasites are highlighted by white arrowheads. B.

1396 *Myxobolus cerebralis* (causative agent of whirling disease) in Giemsa-stained section of

1397 salmonid cranial cartilage (x400 magnification). Parasites are highlighted by black

1398 arrowheads. C. *Hoferellus carassii* infection in H&E stained cyprinid renal tubule

1399 endothelium (x100 magnification). Parasites are present extensively throughout the dilated

1400 tubule lumen (*). D. Haemorrhage and necrotic epithelial cell death within H&E stained
1401 salmonid gill tissue as a result of exposure to hydrozoan organism *Apolesia uvaria* (x200
1402 magnification). Cellular sloughing as a result of tissue trauma can be seen. Histological
1403 sections are from archived material at Cefas including from the Registry of Aquatic
1404 Pathology (RAP) ([https://www.cefas.co.uk/data-and-publications/registry-of-aquatic-](https://www.cefas.co.uk/data-and-publications/registry-of-aquatic-pathology/)
1405 [pathology/](https://www.cefas.co.uk/data-and-publications/registry-of-aquatic-pathology/)) with the exception of image D. Image D credit to Hamish Rodger, vetaqua.com.

1406

1407 **Figure 3: The jellyfish challenge to aquaculture: Varied impacts on fish health from**
1408 **Coelenterata.**

1409 Sessile cnidarian biofouling organisms growing on underwater structures and medusoid
1410 Hydrozoa and Scyphozoa commonly described as ‘jellyfish’ can all impact fish health. Their
1411 contact with aquaculture and impacts are summarised here. Ctenophora (‘comb jellies’) and
1412 parasitic Cnidaria such as Myxozoa, although not generally considered jellyfish, are also
1413 included due to their impact on fish health.

1414

1415 **Figure 4: Clinical consequences of jellyfish exposure.**

1416 Gross lesions from jellyfish bloom exposure in Atlantic salmon. Petechial haemorrhaging
1417 within gill tissue (A) and erosive epidermal damage to skin (B) are reported in fish following
1418 environmental exposure to jellyfish (image credit: Hamish Rodger, vetaqua.com)

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1426 **Table 2 Jellyfish densities associated with harm to fish health**

1427

Cnidarian organism	Known density of negative impact	Negative impact	Citation
<i>Cyanea capillata</i> (Lion's mane); Scyphozoa.	2.5 - 5 g/L (2 hour exposure) *	Acute (0-3 days) Behavioural: <ul style="list-style-type: none">○ Flashing○ Increased rapidity of swimming / hyperactivity Clinical: <ul style="list-style-type: none">○ Skin discolouration○ ‘Whip-lash’ marks Blood biochemistry: <ul style="list-style-type: none">○ ↑Na⁺○ ↑K⁺○ ↑HCO₃⁻ Haematocrit:	(Powell et al., 2018)

		<ul style="list-style-type: none"> ○ ↓Packed cell volume (PCV) <p>Histopathology:</p> <ul style="list-style-type: none"> • Gills <ul style="list-style-type: none"> ○ focal haemorrhages** ○ multifocal hyperplasia** ○ inflammatory infiltration ○ epithelial lifting and oedema** <p>Chronic (3 days +)</p> <p>Haematocrit:</p> <ul style="list-style-type: none"> ○ ↓Packed cell volume (PCV) <p>Histopathology:</p> <ul style="list-style-type: none"> • Gills: Focal hyperplastic lamellae, resolving thrombi. 	
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	(* <i>Salmo salar</i> ; approx. 150g, housed 34 ppt at 12 °C)	(** increased number / extent and severity at higher concentration)	
<i>Aurelia aurita</i> (Moon jellyfish); Scyphozoa.	6 g / L (10 hour exposure) *	Acute (0-3days) Clinical: <ul style="list-style-type: none">Gill: Grossly visible haemorrhages and necrosis of gill tissue Histopathology: <ul style="list-style-type: none">Gills: Epithelial necrosis and sloughing. Multifocal oedema, haemorrhage and cellular hypertrophy progressing to inflammatory infiltration and instances of epithelial stripping. Peak pathology ~24hours	(Baxter et al., 2011b)

		<p>post-exposure. Scored using Mitchell et al quantitative scoring method (Mitchell et al., 2010)</p> <p>Chronic (3 days+)</p> <p>Histopathology:</p> <ul style="list-style-type: none"> • Gill: Lamellar fusion, hyperplasia and inflammation. Scored using Mitchell et al quantitative scoring method (Mitchell et al., 2010). 	
	(* <i>Salmo salar</i> ; approx. 70g, housed 33 ppt at 11 °C)		
<i>Pelagia noctiluca</i> (Maive stinger); Scyphozoa.	1.2 g/L (10 jellyfish / m ³) - 5.8 g/L (50 jellyfish / m ³) (8-hour exposure)*	<p>Acute (0-3days)</p> <p>Clinical:</p> <ul style="list-style-type: none"> • Gill: <ul style="list-style-type: none"> ○ Depigmentation and necrosis ○ Haemorrhage ○ Increased mucus production 	(Bosch-Belmar et al., 2016a)

		<ul style="list-style-type: none"> • Skin <ul style="list-style-type: none"> ○ Macroscopic lesions <p>Behavioural:</p> <ul style="list-style-type: none"> ○ Respiratory distress ○ Jumping ○ Surface swimming <p>Histopathology:</p> <ul style="list-style-type: none"> • Gills: Increased pathological scores according to Mitchell et al scoring system (Mitchell et al., 2012)**. Peak high exposure pathology at 2 days. <p>Chronic (3 days +)</p> <p>Histopathology:</p>	
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	(* Sparus aurita, approx. 200g, housed 37 ppt at 15.5 °C)	<ul style="list-style-type: none"> • Gills: Increased gill scores according to Mitchell et al scoring system (Mitchell et al., 2012. • Skin: Necrosis and inflammatory infiltration with oedema and spongiosis of epithelial tissue <p>(** greater speed of onset and extended recovery times at higher concentration)</p>	
<i>Chrysaora plocamia;</i> Scyphozoa	Unknown	Unclear	(Bosch-Belmar <i>et al.</i> , 2020)
<i>Phacellophora camtschatica;</i> Scyphozoa	Unknown	Unclear	(Bosch-Belmar <i>et al.</i> , 2020)
<i>Phialella quadrata;</i> Hydrozoa.	Unclear density of exposure over 4 days*	Histopathology:	(Bruno and Ellis, 1985)

	(* <i>Salmo salar</i> , approx. 270g, 13 °C marine environment)	<ul style="list-style-type: none"> Gills: Epithelial stripping and necrosis. Leucocytic infiltration and degranulation of eosinophilic cells. 	
<i>Muggiaea atlantica</i>; Hydrozoa.	> 600 jellyfish / m ³ (> 20 jellyfish / m ³)	Increased probability of mortality	(Kintner & Brierly, 2018) (Bosch-Belmar et al., 2017a)
<i>Ectopleura larynx</i>; Hydrozoa.	~20 – 25 g / m ² (35-40,000 polyps / m ² net surface) following four weeks of net growth. 270 polyps/L (112 500 polyps / m ² of net) from net power washing	Acute (0-3days) Clinical: <ul style="list-style-type: none"> Gill: <ul style="list-style-type: none"> Grossly visible changes consistent with a score of 1 in a modified scoring system from Taylor et al. (Taylor et al., 2009). Focal haemorrhages 	(Baxter et al., 2012b) (Bloecher et al., 2018)

		<ul style="list-style-type: none"> • Increased corneal opacity some fish <p>Histopathology:</p> <ul style="list-style-type: none"> • Gills: • Focal epithelial sloughing • Necrosis • Haemorrhage (including thrombi). • Hyperplasia • Average gill score of 4 according to Mitchell at el scoring system (Mitchell et al., 2012) <p>**</p> <p>Chronic (3 days+)</p> <p>Clinical:</p> <ul style="list-style-type: none"> • Gills: <ul style="list-style-type: none"> • Grossly visible changes consistent with a modified scoring system 	
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	<p>(* Salmo salar, approx. 120g, 33ppt at 11 °C)</p>	<p>from Taylor et al of 1 (Taylor et al., 2009) reduced relative to acute impact.</p> <p>Histopathology</p> <ul style="list-style-type: none"> • Gills: • Thrombi and hyperplasia reduced relative to acute impact. • Focal epithelial sloughing and necrosis • Average gill score of 4 according to Mitchell at el scoring system (Mitchell et al., 2012). No significant variation in scores from acute presentation ** <p>** damage also observed in control group of this study, considered to be due to a failure in exclusion of hydroid fragments from recirculation</p>	
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		between challenge groups and controls	
<i>Lizzia blondina</i> ; Hydrozoa.	> 600 jellyfish / m ³	Subsequent gill pathologies and mortalities	(Kintner & Brierly, 2018)
<i>Solmaris spp's</i> ; Hydrozoa.	Unknown	Gills lesions and mortalities	(Baxter et al., 2011a)
<i>Apolemia uvaria</i> ; Hydrozoa.	Unknown	Behavioural: <ul style="list-style-type: none"> ○ Erratic swimming Clinical <ul style="list-style-type: none"> ○ Damage to eyes leading to apparent blindness. ○ Damage to gills ○ Macroscopic skin lesions. ○ Death 	(Bamstedt et al., 1998)
<i>Catablema vesicarium</i> ; Hydrozoa.	Unknown	Unclear	(Purcell et al., 2013)
<i>Porpita porpita</i> (blue button); Hydrozoa.	Unknown	Subsequent mortalities	(Yasudo, 2013)

<i>Verella verella</i> (by-the-wind sailor); Hydrozoa.	Unknown	Increased mortalities	(Rodger et al., 2011)
<i>Aequorea coerulea</i> ; Hydrozoa.	Unknown	Unclear	(Bosch-Belmar et al., 2020)
<i>Bolinopsis infundibulum</i> ; Ctenophora.	Unknown	Unclear	(Bamstedt et al., 1998)
<i>Mnemiopsis leidyi</i> ; Ctenophora.	Unknown	Unclear	(Oppegård 2008)

1428

1429 **Table 2: Gelatinous plankton associated with impaired finfish health; Documented**
1430 **densities and consequences to fish.**

1431 Observed cnidarian jellyfish with documented or suspected negative impact on farmed finfish
1432 species, with densities and exposure periods where available. Environmental surveys and
1433 listed studies of *E. larynx* exposure likely obtain less reliable estimates of exposure density
1434 impact. Concentration of jellyfish exposure is controlled in experimental challenges, but
1435 subject to a degree of variation and error in population estimation of environmental
1436 communities, as well as variable medusal size. Nonetheless, these studies represent the most
1437 quantifiable information available regarding species and densities of concern, providing
1438 important initial findings towards classifying bloom densities in aquaculture. Future research
1439 might quantify blooms as harmful (initiating clinical disease), sub-clinical (impairing fish
1440 health but without immediately apparent negative consequences), and harmless (low-level

1441 presence will likely be considered normal and not of concern, similar to low level

1442 phytoplankton populations).

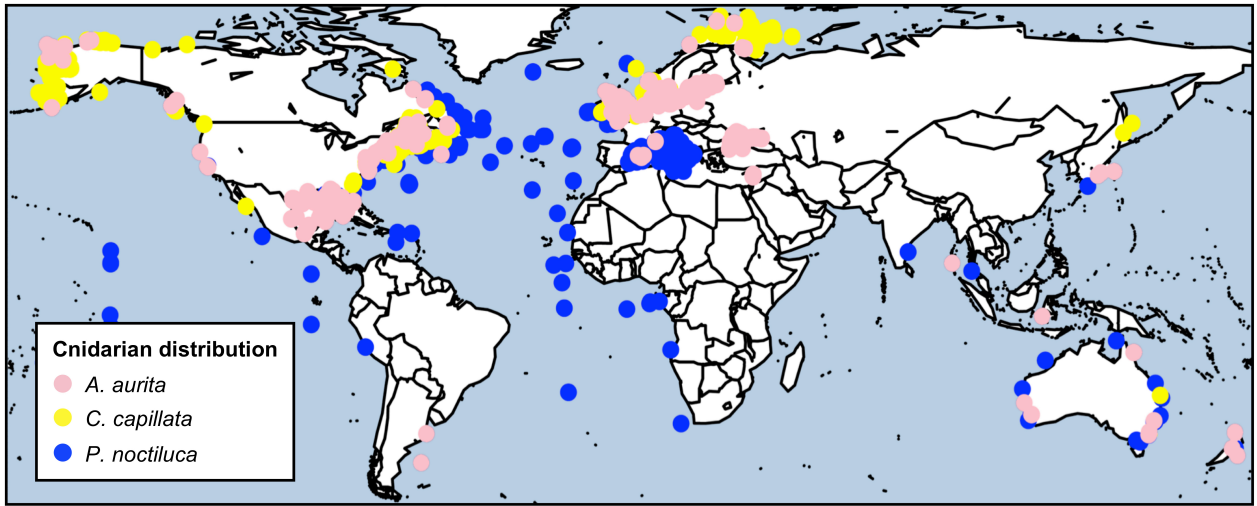
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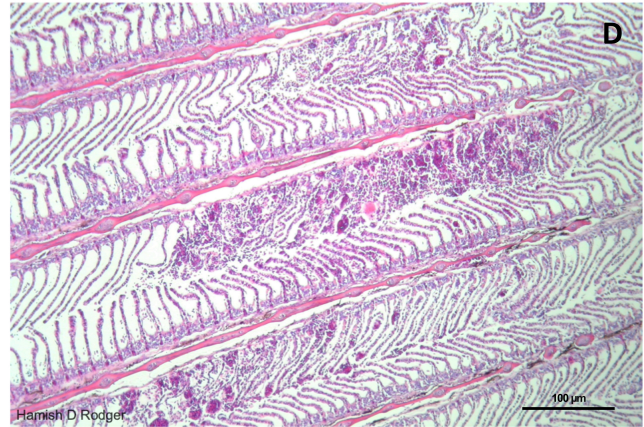
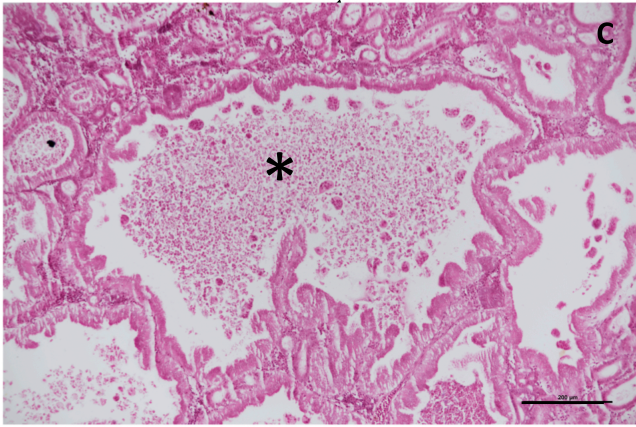
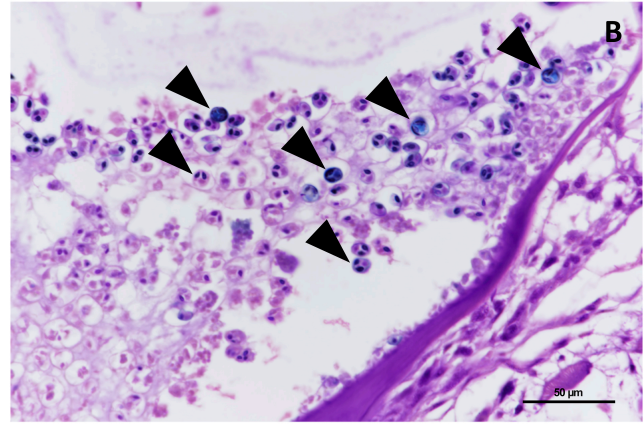
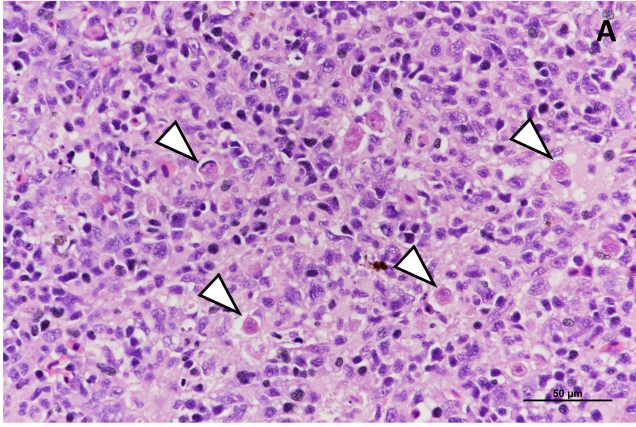
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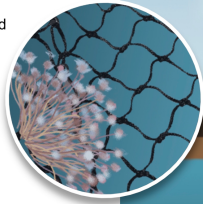
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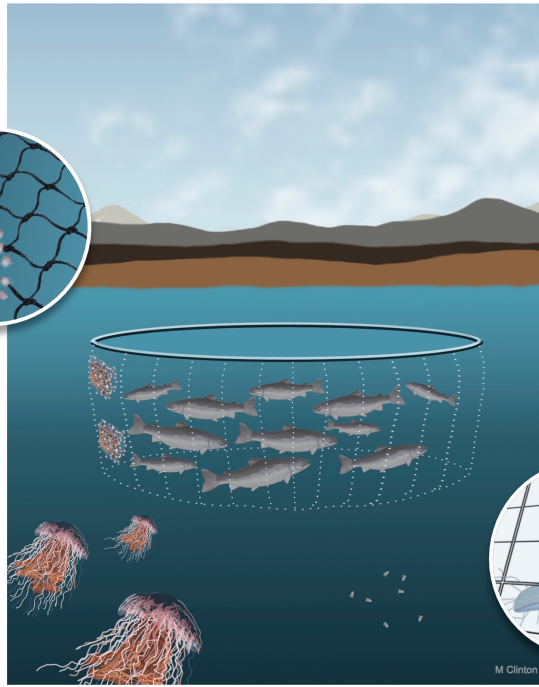
Biofouling cnidarians

Sessile life stages of cnidarian organisms including *E. larynx* can grow on the underwater architecture of aquaculture, such as nets and pontoons. Net-washing can dislodge these organisms into the cage environment, dispersing them throughout the water column. Seasonal budding can also increase cnidarian presence within the net pen.



Medusoid jellyfish (macroscopic)

Larger cnidarian jellyfish including *C. capillata*, *A. aurita* and *P. noctiluca* can cause damage to fish tissue. Strong currents can break jellyfish against nets, allowing macerated tissue to enter cages. Stinging nematocysts then damage fish epithelial tissues, particularly delicate gills. Exposure to *P. noctiluca* has also been linked to subsequent bacterial disease. Clinical disease and even mass mortalities are seen with exposure to large aggregations of bloom forming species.

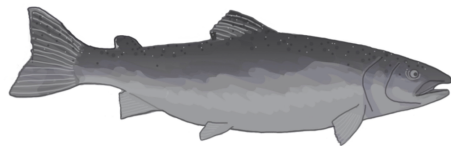
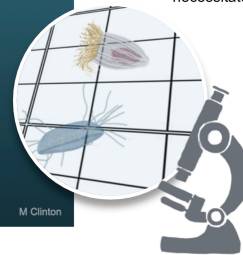


Comb jellies

Ctenophora (comb jellies) are linked in a small number of instances to fish kill events, with the suggested mechanism of oxygen deprivation.

Medusoid jellyfish (microscopic)

Smaller medusoid jellyfish can enter net pens easily through mesh. High presence of microscopic Hydrozoa are associated with increased fish mortalities in farmed stocks, as well as reduced production and disease. Their association with gill pathology necessitates further exploration.



Parasitic cnidarians

Myxozoan parasites of fish are also cnidarian organisms. A number can cause severe disease in aquaculture, including *M. cerebralis* (whirling disease), *T. bryosalmonae* (proliferative kidney disease) and *P. pseudobranchicola*.

Figure 3

