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Size-dependent escape risk of lumpfish (*Cyclopterus lumpus*) from salmonid farm nets --Manuscript Draft--

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Abstract:	<p>In the last decade, the salmon aquaculture industry has considerably increased the use of lumpfish juveniles as cleaner fish. Potential escape of reared lumpfish into the wild may spread diseases or genetically contaminate wild stocks. The guidelines for minimum sizes of cleaner fish to use in aquaculture cages are currently based on simple mesh penetration tests. However, these guidelines do not consider the potential compressibility of fish or changes in mesh state due to factors such as sea conditions and maintenance operations. This study shows that the industry-recommended minimum stocking sizes for a given mesh size may result in escape risk and that ignoring fish compressibility and mesh state can lead to underestimation of the lumpfish sizes that are able to escape. Our results can be used to develop new guidelines that will contribute to reduced escape of lumpfish from salmonid farms and lessen the potential environmental consequences.</p>

1 **Size-dependent escape risk of lumpfish** 2 3 4 **(*Cyclopterus lumpus*) from salmonid farm nets**

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30 31 32 33 34 14 **Abstract**

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28 **1. Introduction**

29 The boom of the salmon (*Salmo salar*) aquaculture industry in the last 20 years has led to
30 high densities of fish in sea cages, and this crowding has resulted in challenges with
31 parasitism and disease outbreaks that compromise the sustainability and welfare of the
32 industry (Aaen et al., 2015). The salmon louse (*Lepeophtheirus salmonis*) is a common
33 parasite on wild salmonids, but in high numbers it can cause significant external damage that
34 can lead to serious infections and death (Wootten et al., 1982). It has a huge negative
35 economic impact on salmon farming companies, and in Norway the industry spends millions
36 of dollars every year to remove this parasite from the fish (Torrissen et al., 2013; Abolofia et
37 al., 2017). For years, parasitized salmon have been treated with chemical baths or mechanical
38 treatments (Overton et al., 2019), but these methods can harm the environment and the fish.
39 Therefore, the use of cleaner fish has become increasingly popular (Gonzalez and de Boer,
40 2017; Brooker et al., 2018; Foss et al., 2020).

41 Today, the salmon farmers in Norway use two families of cleaner fish to remove
42 parasites: wrasses (e.g., Ballan wrasse (*Labrus bergylta*) and goldsinny wrasse (*Ctenolabrus*
43 *rupestris*)) and lumpfish (*Cyclopterus lumpus*). Wrasses have been used for many years
44 (Bjørndal, 1991), whereas the use of lumpfish is more recent (Imsland et al., 2014a,b). The use
45 of lumpfish is gaining popularity among farmers because unlike wrasses, which stop feeding
46 at temperatures below 6°C (Sayer and Reader, 1996), they perform well at low water
47 temperatures and can be used for delousing purposes year-round (Imsland et al., 2016). The
48 industry in Norway uses approximately 30 million juvenile lumpfish each year for delousing

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49 purposes (Foss et al., 2020). Juvenile lumpfish are more effective at delousing and have less
50 impact on salmon growth than larger lumpfish individuals (Imsland et al., 2014c; Foss et al.,
51 2020).

52 Juvenile lumpfish are produced by the salmon aquaculture industry. However, the
53 production of these juveniles requires harvesting wild mature individuals for use as
54 broodstock (Powell, et al., 2018a). Until recently, this species was only harvested for its roe
55 (Johannesson 2006; Kennedy et al., 2019), but the demand from the aquaculture industry for
56 mature adult individuals has increased fishing pressure (Powell et al., 2018a) on a species that
57 already is classified as near threatened on the IUCN Red List (Lorance et al., 2015). The
58 increased use of juvenile lumpfish in salmonid farms has raised various environmental and
59 welfare issues as well (Geitung et al., 2020), including potential impact on wild stocks of
60 lumpfish and high mortality rates of them (Imsland et al., 2020; Klakegg et al., 2020). The
61 potential escape of lumpfish from sea cages also is concerning. In a recent review, Powell et
62 al. (2018a) highlighted the need to critically assess the risk of farmed lumpfish escaping from
63 net pens because escapees can interbreed with local populations and result in genetic
64 introgression, as was previously observed for salmonids escaping from farms (Consuegra et
65 al., 2011). There are five genetically distinct lumpfish groups located in the West Atlantic
66 (USA and Canada), Mid Atlantic (Iceland), East Atlantic (Faroe Islands, Ireland, Scotland,
67 Norway and Denmark), English Channel (England) and Baltic Sea (Sweden) and the genetic
68 diversity within these groups is low, meaning that genetic introgression represents a
69 particularly important threat for this species (Whittaker et al., 2018). According to Jonassen
70 et al. (2018) and Treasurer et al. (2018), eggs and lumpfish juveniles are translocated across
71 the north Atlantic and upon escape these fish can pose a threat to local populations. Treasurer
72 et al. (2018) and Bolton-Warberg et al. (2018) reported respectively that approximately 85 %
73 of the lumpfish used in Scotland in 2017 and 70% of the individuals used in Ireland in the

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74 period 2015-2016, were of Icelandic and Norwegian origin and none of them from local
75 origin, meaning that parental source locations likely are mixed.

76 Small lumpfishes are more effective at delousing salmon than larger individuals, which
77 increases the motivation for farmers to employ smaller individuals in the farms (Imsland et
78 al. 2014a,b,c). Imsland et al. (2016) reported that lumpfish with total length between 10 and
79 18 cm (~50–180 g) have good delousing traits, but in Norway the most commonly used sizes
80 are fish between 6 and 9 cm long (~20 and 30 g) (Salmar AS, Personal communication).
81 However, the use of small lumpfish increases the risk of escape through cage nettings.
82 Salmon farmers traditionally used square meshes of 30–50 mm (Moe et al., 2007), but the
83 mesh sizes used in salmon cages can vary greatly. User guidelines are based on mesh
84 penetration tests, but these tests do not properly account for variability in the condition and
85 compressibility of fish of different sizes (Harboe and Skulstad, 2013). Moreover, earlier
86 studies showed that in addition to mesh size, alterations in mesh state can increase the escape
87 risk of fish through netting meshes (Herrmann et al., 2016a; Sistiaga et al., 2020). Square
88 meshes can adopt different shapes and tension states (bars under tension or slack) due to
89 netting manipulation during maintenance operations and variation in sea conditions (e.g.,
90 currents, waves) (Huang et al., 2006; Lader et al., 2008; Sistiaga et al., 2020). The latter
91 represents an increased risk for cages placed in more exposed sea areas, which is a growing
92 trend in the industry due to increased demand for farming sites (Jónsdóttir et al., 2019).

93 Despite the importance of lumpfish as cleaner fish, no scientific study has been conducted
94 to investigate which sizes of this species can be used safely in salmon cages without risking
95 escape. Therefore, the aim of this study was to evaluate the potential effect of mesh size and
96 mesh state on the escape risk of lumpfish and predict the minimum size of lumpfish that can
97 be safely used in aquaculture cages.

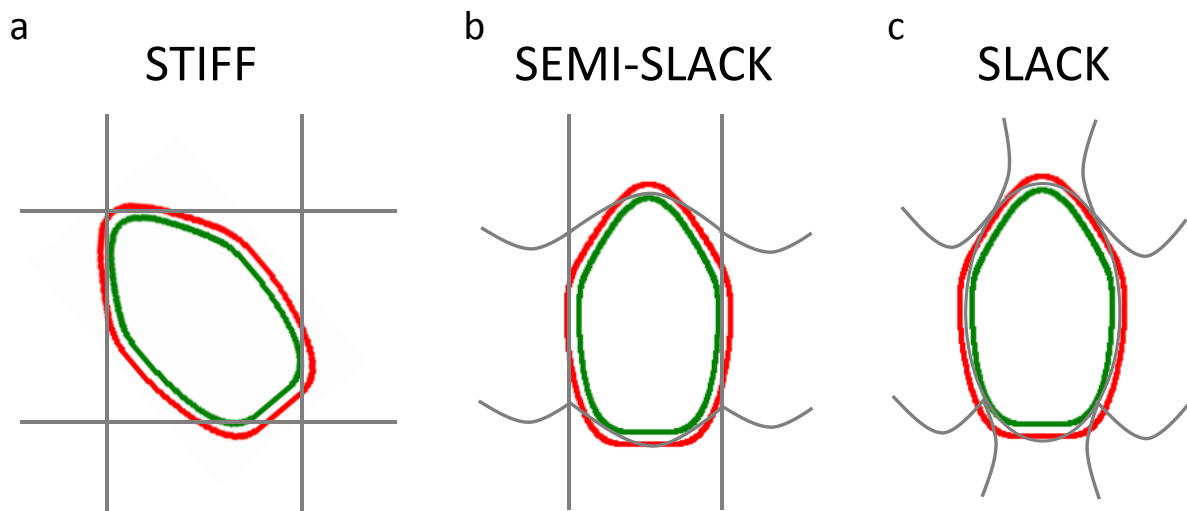
99 **2. Materials and Methods**

100 **2.1. Effect of mesh shape and state vs. lumpfish size and morphology on potential escape**
101 **through cage netting**

102 For a lumpfish to pass through cage netting two conditions must be fulfilled. First, the
103 fish needs to contact the netting at an orientation that gives it a size-dependent possibility of
104 passing through the mesh of the netting (Sistiaga et al., 2010). Second, the fish needs to be
105 morphologically able to pass through the mesh. Therefore, the main factors to consider in the
106 escape risk of lumpfish from fish farming cages are size, shape, and state of the mesh in
107 relation to size, morphology, and tissue compressibility of the lumpfish.

108 To identify the size limits at which fish cannot escape from certain net mesh sizes, the
109 industry carries out penetration tests (Harboe and Skulstad, 2013). In these trials, individuals
110 of a range of sizes are tested on the stretched (stiff) square meshes (Fig. 1a) of the cage to see
111 if they are able pass through them. However, the meshes in the netting of a salmon cage are
112 flexible, meaning that they can be deformed to some extent dependent on mesh bar diameter
113 and twine material stiffness. Further, the meshes adopt different shapes depending on the
114 magnitude and direction of the forces to which they are exposed (Herrmann and O'Neill
115 (2006). These forces depend on factors such as weather and sea currents (Huang et al., 2006;
116 Lader et al., 2003, 2008), thus the mesh state in the netting of cages in exposed locations
117 changes frequently, and the meshes often tend to be in semi-slack and slack states (Fig. 1). In
118 addition, many of the operations performed during cage farming involve manipulation of the
119 cage netting, which again results in the meshes in the netting adopting semi-slack or slack
120 states. In a net panel of square meshes, each with two vertical and two horizontal bars (i.e.
121 sides), hanging at sea, the load in the netting is on the vertical bars due to gravity, meaning
122 that the horizontal bars are to a certain extent tensionless and therefore potentially
123 deformable. When the meshes are semi-slack, the fish in the cages could potentially deform

124 the horizontal bars in the meshes while squeezing through them and ultimately escape (Fig.
125 1b). In situations weather conditions that leads to a sea state with strong sea waves load on
126 the vertical mesh bars will be pulsing, dynamically changing size and direction, potentially
127 resulting in periods where the load on the vertical bars would disappear, making the meshes
128 slack and deformable in all directions (Fig. 1c). Slack and at least some states of semi-slack
129 meshes would lead to a higher risk of escape for lumpfish, simply because the mesh totally
130 (slack) or partially (semi-slack) deforms when adjusting to the shape of lumpfish trying to
131 squeeze through it. Therefore, penetration tests assuming a stable stiff state of the meshes in
132 cage netting likely leads to a serious underestimation of the size of lumpfish that can escape.



134
135 Fig. 1. Mesh penetration of a lumpfish represented by its cross-section (red = uncompressed, green = maximum
136 compression) through a (a) stiff, (b) semi-slack, and (c) slack mesh.

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138 Two factors determine the maximum size at which a lumpfish individual would be able to
139 squeeze through a mesh. The first is the deformability of the meshes in the netting and the
140 second is the deformability or compressibility of the lumpfish tissue. In Figure 1, only a
141 lumpfish with a compressibility level illustrated by the green cross-section (CS) would be
142 able to pass through the square meshes in each of the mesh states (Fig. 1a-c). Thus, different

143 potential netting scenarios in combination with the morphology and cross-sectional
144 compressibility of the species being investigated must be tested to quantify the potential risk
145 of escape for a lumpfish through a specific netting.

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147 **2.2. FISHSELECT methodology and data collection**

148 FISHSELECT (Herrmann et al., 2009, 2012) is a framework of methods, tools, and
149 software developed to determine if a fish can penetrate a certain mesh or defined shape. The
150 method has been widely used to predict the size selectivity of fishing gear (the size-dependent
151 probability for escape/retention) (Krag et al., 2011; Sistiaga et al., 2011; Herrmann et al.,
152 2016a,b; Tokaç et al., 2016; Tokaç et al., 2018; Cuende et al., 2020). In the current study, we
153 used this method for the first time to predict the risk of lumpfish escaping through salmon
154 farm cage netting.

155 Both FISHSELECT software and specific measuring tools are needed to study the size
156 selectivity of a species using this method (Fig. 2). Through computer simulation, the method
157 estimates the risk of escape by comparing the morphological characteristics of a particular
158 fish species and the shape and size of the selection devices of interest. The following
159 subsections briefly describe the different steps needed to use FISHSELECT. A more
160 thorough description of the method can be found in Herrmann et al. (2009, 2012).

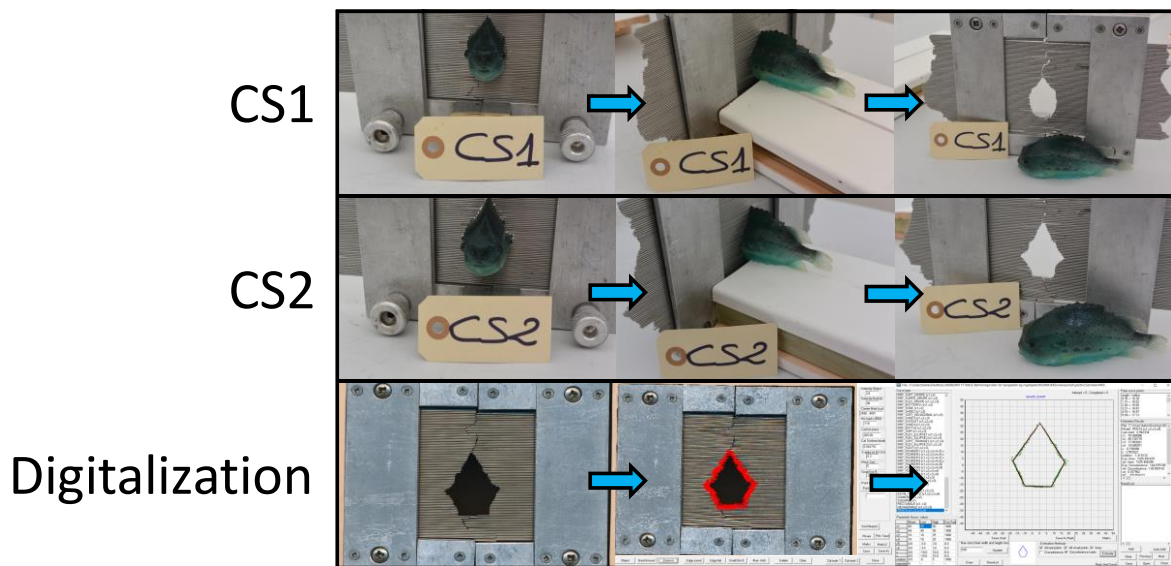
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162 *2.2.1. FISHSELECT morphometric data collection*

163 In addition to measuring the total length and weight of each individual lumpfish included
164 in the study, its cross-sectional morphology was measured at specific points along its length.
165 To obtain the correct morphometric measures for each fish using FISHSELECT, it is important
166 that the shape of the fish measured is not affected by dehydration, depressurization, rigor
167 mortis, or any other factor that could alter the original shape of the fish. Therefore, the fish for

168 the trials were handpicked in batches of 4–5 fish and killed with an overdose of MS 222
169 anaesthetic just before use. Our aim with FISHSELECT was to make predictions for mesh
170 penetration probability for the widest possible range of fish sizes. Thus, apart from the
171 condition of the lumpfish selected, the only other selection criterion for fish was that they
172 covered the widest possible size range.

173 Two cross-sections were selected for their potential to determine fish passage through a
174 mesh: cross-section 1 (CS1), which was located directly behind the operculum, and cross-
175 section 2 (CS2), which was located at the point of the maximum transverse perimeter (i.e., the
176 foremost point of the dorsal fin) (Fig. 2). CS1 represents the point of maximum girth of the
177 bony structure in the head, whereas CS2 represents the point with maximum girth of the fish
178 overall. Thus, these two CSs were expected to be the decisive CSs for mesh penetration. The
179 two cross-sections were measured using a sensing tool called a morphometer. The shapes
180 formed in the morphometer were then scanned to obtain digital images of the contours using a
181 flatbed scanner (Fig. 2).



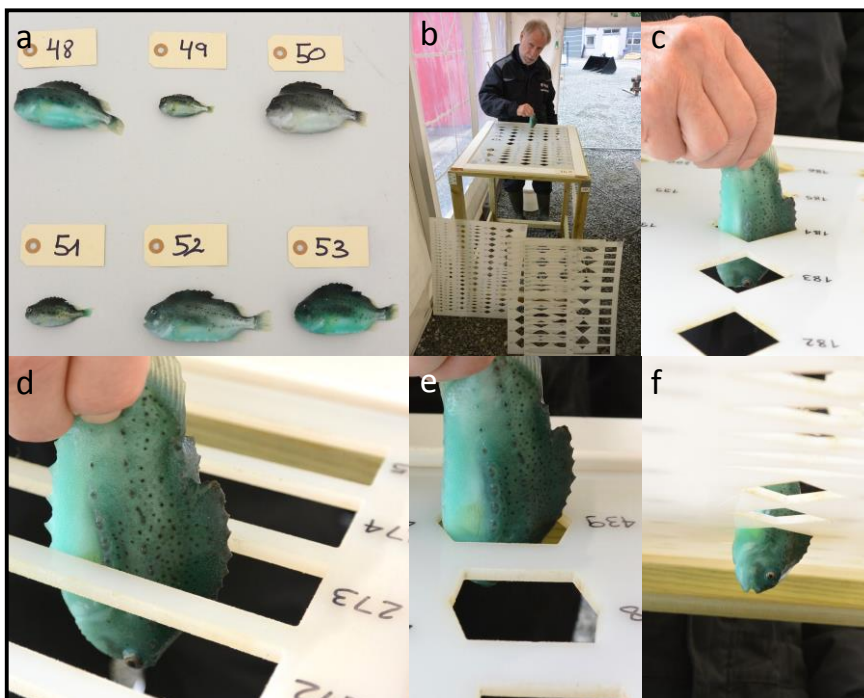
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184 Fig. 2. The first and second rows describe CS1 and CS2, respectively, and the third row shows the process of
185 digitalization of the shapes measured by a morphometer.

186 Models (i.e., numerical representations through parametric shapes) of the digitized cross-
187 sectional images obtained for each lumpfish were developed. For each CS, we initially
188 considered five different shape models: ellipse, flexellipse1, flex drop, super drop, and ship
189 (see Sistiaga et al. (2020) for further information about these five models). The models were
190 selected based on previous experience with other fish species. However, we also had to develop
191 a new model due to the distinctive morphology of lumpfish. This model, which we named
192 penta, is shaped like a pentagon and is defined by four parameters (see the Appendix for further
193 information about the penta model). The Akaike Information Criterion (AIC) (Akaike, 1974)
194 and R^2 values were calculated for each of the six models for both CS1 and CS2 (see Tokaç et
195 al. (2016) for further details about this process). The shape model with the lowest mean AIC
196 value was chosen to describe each of the two cross-sections separately. The mean R^2 value was
197 applied to judge how well the selected models on average described the cross-sectional shapes
198 of lumpfish. The relationship between total length and cross-section shape parameters was
199 modelled for the most suitable shapes found for CS1 and CS2 separately.

200 2.2.2. Fall-through experiments

201 After measuring lumpfish morphology, we conducted fall-through experiments to determine
202 whether each lumpfish included in the study could or could not physically pass through an
203 array of stiff mesh shapes perforated in 5 mm nylon-plate templates. Only the force of gravity
204 was used to simulate the attempted penetration of lumpfish through the mesh (Fig. 3). All
205 lumpfish were presented at an optimal orientation for mesh penetration to each of the 478 meshes in
206 the templates. The set of mesh templates used in this experiment consisted of 478 different
207 shapes representing mesh sizes ranging from 20 to 245 mm. The shapes included diamonds
208 (252 meshes), hexagons (98 meshes), and rectangles (128 meshes) and were identical to those
209 described by Tokaç et al. (2016). All lumpfish were presented at an optimal orientation for
210 mesh penetration to each of the 478 meshes in the templates. Compared to using real meshes

211 for the penetration tests, the cut-out meshes in the mesh templates are much more precise and
212 well-defined in shape and size, which is essential for the precision in the results obtained.
213 Penetration (Yes) or retention (No) was recorded for each fish (see Herrmann et al. (2009) for
214 further details about the procedure). The purpose of the fall-through experiments was to
215 estimate the maximum compressibility for a fish trying to squeeze itself through a mesh (see
216 Herrmann et al. (2009) for further details).



218
219 Fig. 3. Photo (a) shows a sample of the different lumpfish sizes used in the fall-through tests, photo (b) shows
220 the different templates employed in the fall-through tests, and photos (c–f) illustrate the fall-through procedure
221 for different lumpfish and meshes.
222

223 2.2.3. Simulation of mesh penetration and selection of a penetration model

224 The shape and compressibility of a lumpfish determines whether it will be able to pass
225 through a mesh. The penetration models implemented in FISHSELECT simulated the
226 compressibility of each fish at each cross-section. Visual and tactile inspection of the
227 deformability of lumpfish revealed that the dorsal and ventral compressibility of this species
228 may differ. Therefore, we applied a model that allows asymmetrical compression for both

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229 CS1 and CS2. Herrmann et al. (2012) previously used this model for redfish (*Sebastes* spp.),
230 and it includes the estimation of three parameters that represent the dorsal, lateral, and ventral
231 compressibility of the fish. The potential compressibility of the fish at an arbitrary angle
232 around the fish cross-section was then modelled by linear interpolation between the potential
233 compressibility (dorsally, laterally, and ventrally) of the fish at each cross-section (see
234 Herrmann et al. (2009) for further details).

235 To establish an optimal penetration model for lumpfish, each CS1 and CS2 measurement,
236 both individually and in combination, was tested with different compression models using
237 different values for the assumed dorsal, lateral, and ventral compression. The penetration of
238 the modelled CS1 and CS2 shapes of each fish through the 478 different mesh templates used
239 in the fall-through trials was simulated using the FISHSELECT software. The purpose of
240 these simulations was to estimate the compression potential of the cross-sections and to
241 assess which cross-section combinations needed to be considered when estimating the
242 potential for lumpfish to pass through meshes of different sizes and shapes. Models
243 considering one cross-section at a time were created. For CS1, the dorsal, lateral, and ventral
244 compression varied from 0 to 20%, 0 to 30%, and 0 to 30%, respectively, in increments of
245 5%. This resulted in 245 penetration models for CS1. For CS2, the dorsal, lateral, and ventral
246 compression varied from 0 to 30%, 0 to 20%, and 0 to 40%, respectively, in increments of
247 5%. This resulted in 315 penetration models for CS2. In addition to the models run for each
248 cross-section, 77,175 models in which CS1 and CS2 were combined were also tested. Each
249 compression model was used to simulate fall-through results for each of the meshes and fish
250 used in the experimental fall-through data collection (Section 2.2.2). Using the FISHSELECT
251 software, the results obtained from all different penetration models were compared with our
252 experimental fall-through results. This evaluation produced a value for the degree of

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2 253 agreement (DA value), which expresses the percentage of the fall-through results for which
3 254 the simulated results were the same (“yes” or “no”).
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7 256 *2.2.4. Modelling of mesh shapes for square meshes in fish farm cages during lumpfish escape*
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9 257 *attempts*
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12 258 Before being able to use the generated virtual population of lumpfish and the identified
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14 259 penetration model to predict the risk of lumpfish escape through square meshes in fish farm
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16 260 cages using the FISHSELECT methodology, we needed an appropriate model for the semi-
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18 261 slack mesh state (Fig. 1b) and for the fully slack mesh state (Fig. 1c). In the FISHSELECT
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20 262 simulation, the latter is directly modelled by the condition that a lumpfish can escape if the
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22 263 circumference of its cross-section under maximum compression is less than the inner
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24 264 circumference of the mesh it attempts to pass through. This is because the mesh in this mesh
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26 265 state will be fully distorted while the lumpfish is passing through it. In semi-slack and partly
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28 266 open square meshes (Fig. 1b), the shape the mesh will take when a fish attempts to pass
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30 267 through it was approximated by a hexagonal shape wherein the tensionless horizontal mesh
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32 268 bars are bent upwards and downwards (Fig. 4a–c). This approximation has been applied
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34 269 successfully when modelling fish escape through square mesh codends in trawl and demersal
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36 270 seine fisheries for several species including salmon smolt (Sistiaga et al., 2020), cod
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38 271 (Herrmann et al., 2016a, 2016b), haddock (Krag et al., 2011; Herrmann et al., 2016b), red
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40 272 mullet (Tokaç et al., 2016), and hake (Tokaç et al., 2018).
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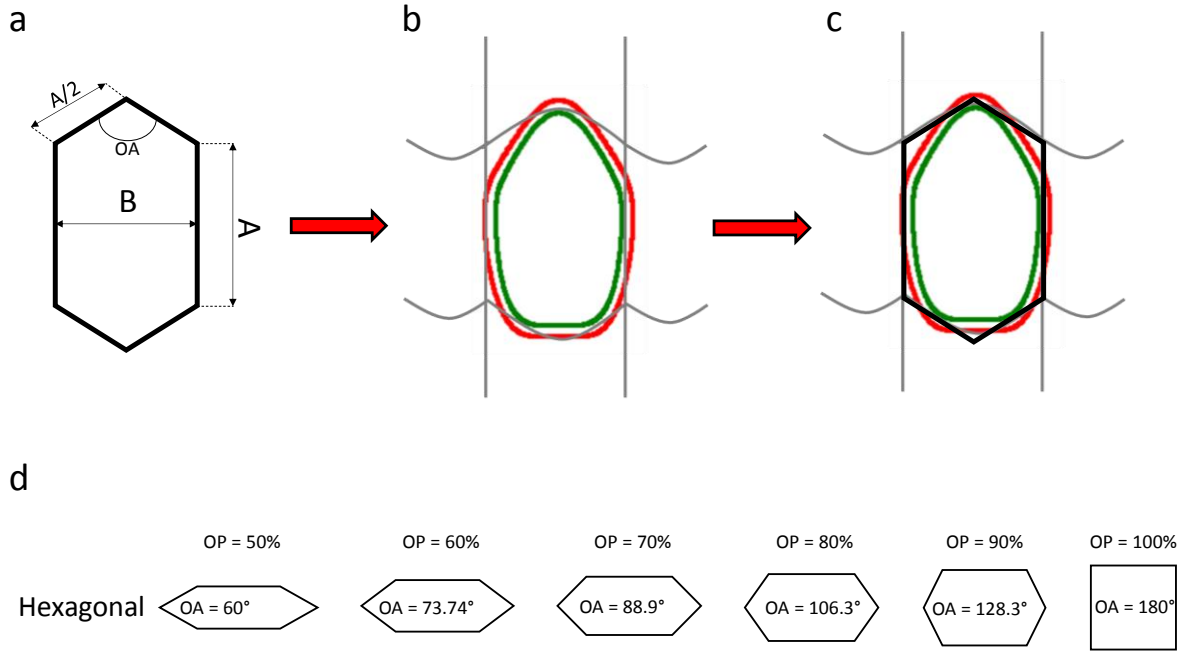


Fig. 4. Hexagonal mesh shape approximation for fish escape through a semi-slack square mesh. (a) Details about hexagonal mesh. (b) Illustration of fish escape through semi-slack square mesh. (c) Approximation of the distorted semi-slack square mesh with a hexagonal shape. (d) Examples of hexagonal shapes approximating distorted semi-slack square meshes with different levels of openness (see Eq. (1)). A = mesh bar length. B = mesh width. OA = opening angle. OP = relative openness.

We applied two related measures to describe the openness of a hexagonal modeled distorted semi-slack square mesh: opening angle (OA) and relative openness (OP). They quantify the circumferential (horizontal) opening of the mesh (B) relative to the vertical opening (A) (Fig. 4a). Figure 4d shows the relationship between OA and OP for hexagonal distorted square meshes, which is calculated as follows:

$$OP = 100 \times \frac{B}{A} = 100 \times \sin\left(\frac{OA}{2}\right) \quad (1)$$

The stiff mesh scenario (Fig. 1a) is a special case for the hexagonal approximation of the semi-slack mesh when $OA = 180^\circ$ corresponding to an OP of 100%.

2.2.5. Quantifying the escape risk

290 Based on the morphological description of CS1 and CS2 (section 2.2.1.), a virtual population
 291 of 2000 lumpfish with uniformly distributed length of up to 25 cm was created to simulate
 292 size selection. This upper size limit was selected because predictions for meshes up to 100
 293 mm were desired. For all three mesh scenarios (Fig. 1) the risk of lumpfish escape was
 294 simulated for square meshes with a mesh size between 10 and 100 mm in increments of 5
 295 mm. For the semi-slack scenario, approximated by a hexagon, OP values from 50 to 100%
 296 were used in increments of 5%. Using the identified lumpfish penetration model, a simulation
 297 was created to determine whether each individual in the virtual population could pass through
 298 the mesh in each of the mesh scenarios (stiff, semi-slack, slack). Likewise, for the standard
 299 application of the FISHSELECT method (Herrmann et al., 2009) we obtained for each mesh
 300 a virtual size selection dataset consisting of lumpfish size-dependent counts of individuals (in
 301 1 cm wide length classes) from the virtual population being retained (not able to pass
 302 through) and released (being able to pass through), respectively. We then fitted the traditional
 303 logit size selection model to the size selection data by maximum likelihood estimation to
 304 obtain the values for the model parameters $L50$ and SR as follows (Wileman et al., 1996):

$$\text{logit}(l, L50, SR) = \frac{\exp\left(\frac{\ln(9)}{SR} \times (l - L50)\right)}{1 + \exp\left(\frac{\ln(9)}{SR} \times (l - L50)\right)} \quad (2)$$

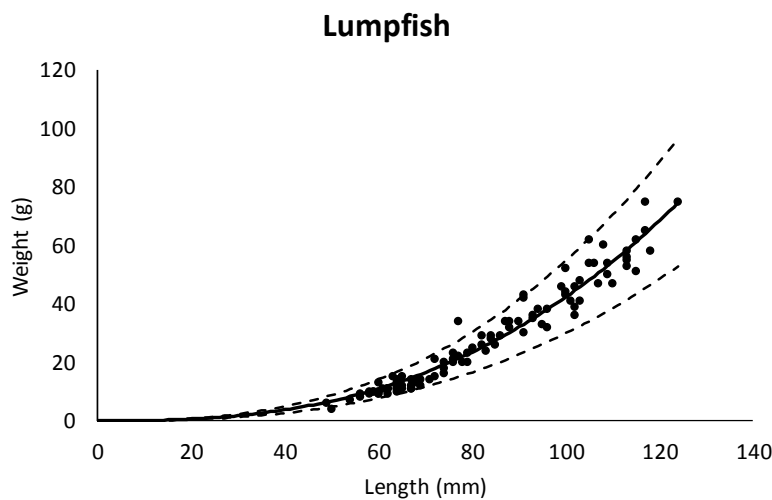
306 where $L50$ quantifies the length of lumpfish that have a 50% probability of being retained and
 307 the selection range (SR) is the difference between $L75$ and $L25$ (Wileman et al., 1996). Based
 308 on the obtained size selection curves, the size of lumpfish having a 99% retention probability
 309 ($L99$; maximum 1% escape risk) was calculated and used as a measure for the minimum safe
 310 size that could be kept in the cages. For a logit size selection model, $L99$ can be calculated as
 311 follows (Krag et al., 2014):

$$L99 = L50 + \frac{SR}{\ln(9)} \times \ln(99) \quad (3)$$

313 3. Results

314 3.1. Data collection

315 The morphology data collection and fall-through experiments were conducted at a
316 lumpfish juvenile rearing plant in Trøndelag (Mid-Norway) in June 2017. During the study
317 period we had continuous access to live fish, which facilitated selection of the individuals
318 necessary to cover the widest possible size span of lumpfish. The FISHSELECT procedure
319 was applied to 100 lumpfish between 49 mm (6 g) and 124 mm (75 g) (Fig. 5).



325 Fig. 5. Weight vs. length relationship for the 100 lumpfish included in the study ($W = a \times L^b$). $a = 2.2249 \times 10^{-4}$
326 and $b = 2.64$. $R^2 = 0.9488$. The stippled lines show 95% confidence intervals.

327 3.2. Cross-section model choice and compressibility of lumpfish

328 Using computer simulation, the six models considered (section 2.2.1.) were tested on the
329 CS1 and CS2 experimental data to determine which model was best able to describe each CS.
330 The model that resulted in the lowest AIC value was chosen in each case. The model ship,
331 which is a 3-parameter model, was the best representation for CS1, whereas CS2 was best
represented by the model penta, which is a 4-parameter model (Table 1). In both cases the R^2
was > 0.94 , meaning that the model was able to describe CS1 and CS2 well.

332 During the fall-through experiments, each lumpfish was tested through 478 meshes of different
 333 sizes, meaning that during the experimental period a total of 47,800 fall-through trials were
 334 carried out with the 100 fish selected. We used these fall-through results and computer
 335 simulation to determine the maximum compression levels for CS1 and CS2. The highest DA
 336 between the experimental and simulated fall-through results when considering only the
 337 compressibility at CS1 was 97.58%, whereas the highest DA when considering only the
 338 compressibility at CS2 was 96.35%. When both CS1 and CS2 were considered, the highest DA
 339 achieved was 97.65%. Therefore, this combined compression model was chosen for further
 340 analysis and to make mesh penetration predictions for lumpfish in FISHSELECT. The model
 341 had a dorsal compression of 5%, lateral compression of 0%, and ventral compression of 0%
 342 for CS1 and a dorsal compression of 15%, lateral compression of 10%, and ventral compression
 343 of 20% for CS2 (Fig. 6).

344 Table 1. Comparison of the performance of the six different models tested on the CSs (all models except for penta,
 345 which is described in the Appendix, are described in Sistiaga et al., 2020).

CS models	Ellipse		Flex Ellipse 1		Penta		Super Drop		Flex Drop		Ship	
	CS1	CS2	CS1	CS2	CS1	CS2	CS1	CS2	CS1	CS2	CS1	CS2
AIC	310.00	470.29	271.04	436.61	276.51	300.28	268.06	434.01	264.03	403.85	252.41	408.67
Nr parameters	2	2	3	3	4	4	3	3	3	3	3	3
R ²	0.9050	0.7653	0.9328	0.8225	0.9301	0.9402	0.9334	0.8247	0.9361	0.8633	0.9419	0.8584

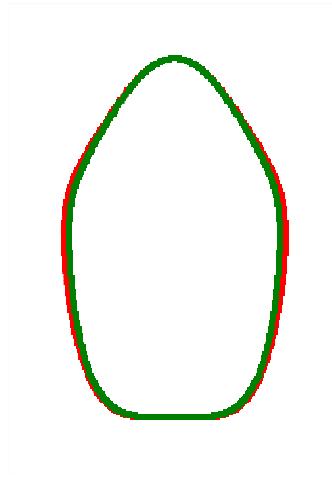
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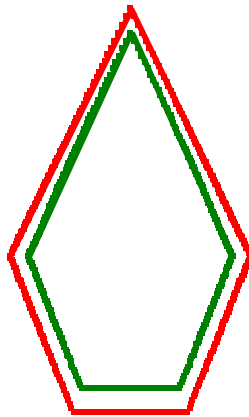
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CS1



CS2



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349 Fig. 6. The combined compression model that provided the highest DA illustrated for one of the 100 lumpfish
350 included in this study. The red contour represents the uncompressed CS, and the green line represents the CS with
351 maximum compression.

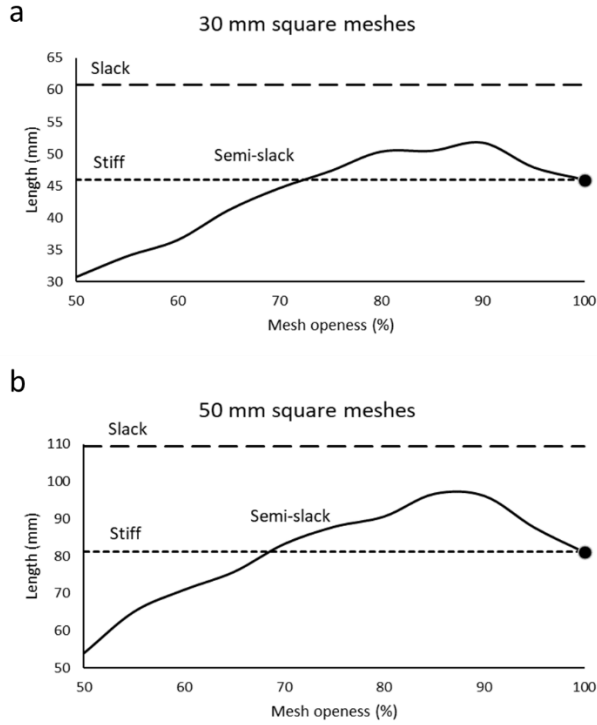
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353 3.3. Predictions of mesh penetration and escape risk

354 Based on a virtual population of 2000 fish, we predicted the escape risk of lumpfish
355 through square meshes of 30 and 50 mm, which are two mesh sizes often used by the
356 salmonid aquaculture industry in Norway. The results showed that if the meshes in the cage
357 netting are completely stiff and perfectly square, lumpfish of up to 46 and 81 mm would be
358 able to escape (< 1% risk) through meshes of 30 and 50 mm, respectively (Fig. 7). In
359 contrast, if the meshes in the cage are completely slack and fully deformable, the escape risk
360 for lumpfish would be higher and fish of up to 61 and 109 mm would be able to escape (< 1%
361 risk) through meshes of 30 and 50 mm, respectively (Fig. 7). If the meshes in the cage are
362 semi-slack, meaning that only the horizontal bars in the meshes are deformable, the escape
363 risk would vary depending on the mesh openness (deformation level of the horizontal bars).
364 For square meshes of 30 mm, the lumpfish size with < 1% escape risk increases to ~52 mm
365 with a mesh openness of ~90% and decreases to 46 mm when the meshes are 100% open
366 (perfectly square meshes). For square meshes of 50 mm, the lumpfish size with < 1% escape

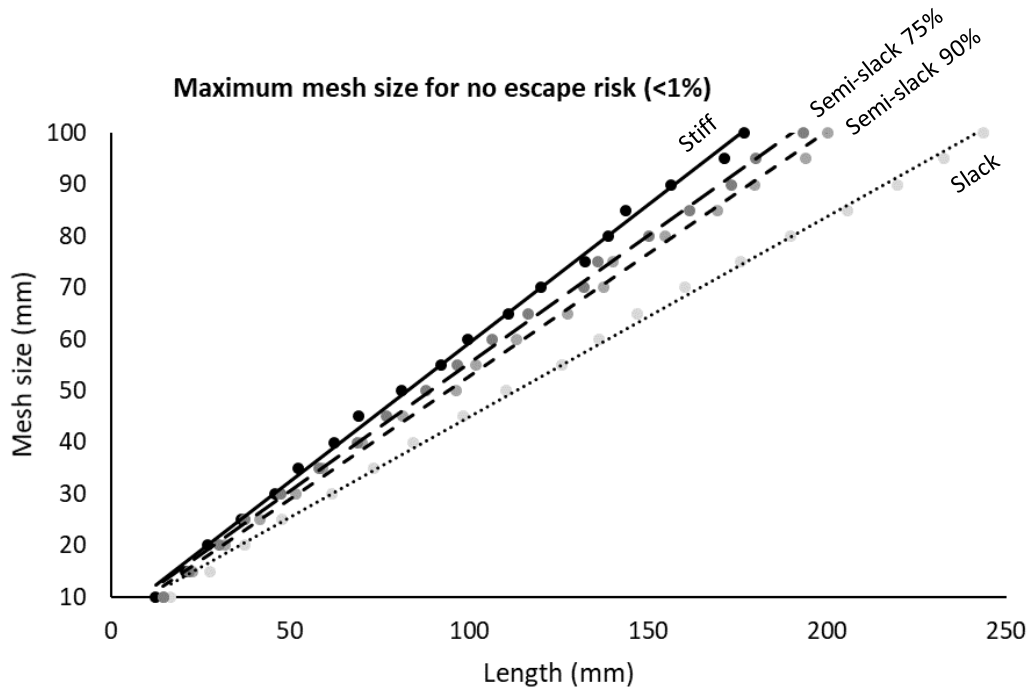
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3 367 risk increases to ~96 mm with a mesh openness of ~90% and decreases to 81 mm when the
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5 368 meshes are 100% open (perfectly square meshes).

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7 369 The plot in Figure 8 illustrates the minimum size of lumpfish (L99) that can be used for
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9 370 meshes of different sizes and four different states (stiff, semi-slack with 75% mesh openness,
10 371 semi-slack with 90% mesh openness, and slack meshes). The results clearly show that square
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12 372 meshes in the stiff state allow safe use of the smaller sizes of lumpfish as cleaner fish in the
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14 373 salmon cages without risk of escape into the wild, whereas the meshes need to be
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16 374 substantially reduced in size to maintain the same safety level if the meshes in the cage
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18 375 netting are slack or semi-slack (Fig. 8). For example, to safely retain lumpfish ≥ 150 mm
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20 376 long, the meshes in the cage netting would have to be ≤ 62 mm if the meshes are completely
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22 377 slack at times. However, if the meshes are always stiff, this mesh size could be increased to
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24 378 ~85 mm with the certainty that no fish > 150 mm long would escape. For semi-slack meshes,
25
26 379 escape risk with mesh openness $> 75\%$ is higher than that of stiff meshes but lower than that
27
28 380 of slack meshes. The escape risk for semi-slack meshes is closest to that of slack meshes
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30 381 when the former have an openness of ca. 90%. This pattern was similar for the whole mesh
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32 382 size range considered (10–100 mm) (Fig. 8).
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384 Fig. 7. Sizes of lumpfish with escape risk < 1% (Y axis) as a function of mesh openness (X axis) for semi-slack
 385 meshes (solid line). The dashed lines represent the results for slack meshes, and the stippled lines represent the
 386 results for stiff meshes. Plot (a) shows the results for 30 mm square meshes and plot (b) shows the results for 50
 387 mm square meshes.



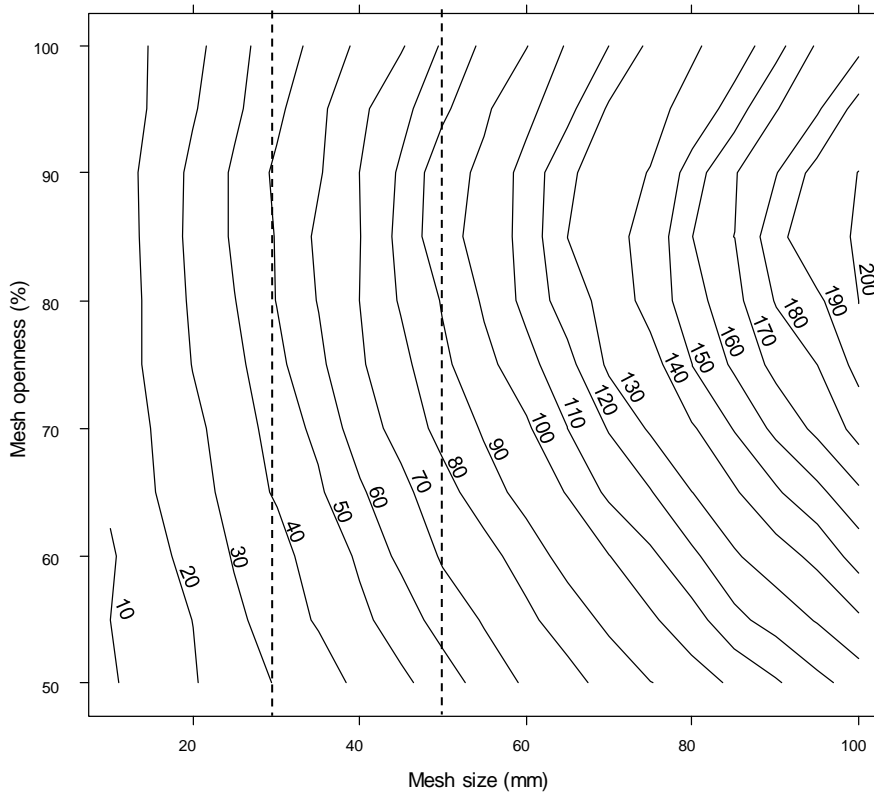
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389 Fig. 8. Maximum square mesh size that guarantees < 1% escape risk as a function of lumpfish size. The lines in
1 390 the plot show the limits for stiff meshes (full line), slack meshes (dotted line), and semi-slack meshes with 75 and
2 391 90% mesh openness (dashed and stippled lines, respectively).

392 The isolines in the design guide (DG) (Fig. 9) show the smallest sizes of lumpfish that
393 can be safely used (escape risk < 1%) at different mesh size and openness. The DG clearly
394 shows that larger mesh size requires the use of larger lumpfish, independent of mesh
395 openness, to avoid escape risk. Figure 8 also shows that the escape risk for semi-slack meshes
396 with a high degree of openness is larger than for square stiff square meshes (100% openness).
397 For all mesh sizes considered, escape risk increases with mesh openness up to ~90%, and
398 then it decreases to 100% openness, with the same risk as that for square stiff meshes. Thus,
399 if the netting in the cages is changed from 30 mm square meshes to 50 mm square meshes,
400 the minimum size of lumpfish used in the cage should be increased by ~40 mm to maintain
401 an escape risk < 1%, independent of mesh openness.

Minimum length to avoid escape risk versus mesh size and openness



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403 Fig. 9. Isolines showing minimum length of lumpfish (< 1% escape risk) in mm that can be used in farms for
404 square meshes between 20 and 100 mm and mesh openness varying between 50 and 100% in the semi-slack mesh
405 state. The stippled lines show the estimates for the 30 and 50 mm meshes that can be related to Fig. 7.

406

407 **4. Discussion**

408 Several studies have highlighted the importance of limiting the escape of lumpfish from
409 salmon farming cages (Powell et al., 2018a; Whittaker et al., 2018) to avoid potential
410 problems such as spreading of diseases, outcompeting endemic species, and genetic
411 contamination of surrounding ecosystems (Consuegra et al., 2011; Sepulveda et al., 2013). In
412 the Norwegian aquaculture industry, which is the largest “consumer” of juvenile lumpfish
413 worldwide (Foss et al., 2020), the mesh sizes used in net cages and how they relate to the
414 minimum sizes of lumpfish used are not regulated by law. Farmers use self-developed
415 guidelines based on mesh penetration tests that do not consider potential variations in fish
416 compressibility or different mesh states, which can lead to underestimation of the minimum
417 lumpfish size needed for each mesh size, which in turn may permit escape of reared lumpfish
418 into the wild. Although the extent to which lumpfish escapees occur is not reported in
419 literature, it is acknowledged that this is a problem for the industry that needs to be
420 investigated (e.g. Powell et al., 2018).

421 In this study, we evaluated the escape risk of lumpfish from salmon farms based on the
422 morphology of the species and the size and state of the meshes used in cage nets. The
423 Norwegian industry typically uses meshes of 30 and 50 mm in the cage nettings (Moe et al.,
424 2007), and the sizes of lumpfish employed can be as low as 6–9 cm in length (Salmar AS,
425 Personal communication). For square meshes of 30 mm, which are often used in the cage
426 nettings, our results show that even the most critical mesh state (slack) would not lead to any
427 significant escape risk (< 1%), as the minimum safe size is estimated to be 6.1 cm. However,
428 for cage nets with 50 mm meshes, the use of 6–9 cm long lumpfish would be of concern.

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429 Even at the least critical mesh state (stiff), lumpfish < 8.1 cm would pose an escape risk.
430 Therefore, to avoid escape risk and the associated risk of biological contamination, lumpfish
431 as small as 6–9 cm should only be used when the mesh size in the net cages is 30 mm.
432 According to our results, use of the 50 mm mesh would only be safe for lumpfish > 11 cm in
433 situations where the meshes likely would go slack at times. For the slack and semi-slack
434 mesh state our predictions assume that lumpfish are able to deform the tensionless mesh bars
435 in the cage netting. In practice, the extent to which lumpfish can do this may depend on the
436 bending stiffness of the mesh bars in the cage netting (Herrmann and O'Neill, 2006). Our
437 results can be seen as “worst-case scenarios”, but they represent the cases that need to be
438 considered in a precautionous estimate for escape risk. For the industry, a cautious approach
439 that guarantees a 0-escape scenario through mesh penetration is recommended. This can be
440 achieved by increasing the smallest sizes of lumpfish used a certain percentage above the
441 limits established here, or reducing the mesh sizes further from the limits established,
442 although the latter may imply additional challenges and require trade-offs regarding issues
443 like water flow, fouling, etc.

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444 Compared to other relevant species in the aquaculture industry (e.g. smolt (Sistiaga et al.,
445 2020)), lumpfish are not particularly compressible. Furthermore, they are not good swimmers
446 (Powell et al., 2018b), which suggests limited power to squeeze themselves through meshes.
447 These two characteristics suggest that our escape risk results likely are not underestimated.
448 Our results also illustrate that changes in mesh state (openness) can have dramatic
449 consequences for the penetrability of lumpfish through square meshes (Figs. 7–9), and these
450 changes are not considered in the industry guidelines. The consequence of not considering
451 mesh state is clearly shown in Figure 9. For example, the industry guidelines state that
452 salmon farmers should be able to use lumpfish as small as 67 mm with square meshes of 40
453 mm (Sigstadstø, 2017). Although this result is in good agreement with our estimations for

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454 stiff square meshes, fish > 67 mm long would be able to escape through the 40 mm meshes
455 with mesh openness of 75–95%. Thus, if the meshes in the cage netting are subjected to
456 deformation due to factors such as sea state, sea currents, or maintenance operations in the
457 farm but the minimum size allowed is based on the assumption that escape only occurs
458 through stiff square meshes, there could be substantial risk of lumpfish escape.

459 Because farmers prefer to use small lumpfish, it is likely that the lumpfish added to the
460 cages are as close to the established lower size limit as possible, which substantially increases
461 the risk of escape. The preference for small lumpfish is driven by their delousing efficiency,
462 which has been reported to decrease with increasing size (Imsland et al., 2014a,b,c).
463 Additional advantages include shorter rearing time (costs) and the possibility for coexistence
464 with wrasses, which can be harassed by larger lumpfish (Imsland et al., 2016). However,
465 smaller inexperienced lumpfish show more avoidance behavior towards salmon than larger
466 individuals (Staven et al., 2019). This initial behavior of avoiding contact with salmon can
467 lead small lumpfish to attempt escape from the cages. If this potential fleeing behavior is
468 added to the inherent increase in escape risk due to their smaller size, the sustainability of
469 using the smallest sizes of lumpfish is questionable.

470 The escape of lumpfish from aquaculture cages has multiple implications. For example,
471 escape increases the cost for the industry, as lumpfish escapees need to be replaced to
472 maintain delousing capacity. However, the most important socio-economic implication of
473 losing reared lumpfish to the wild is related to the potential environmental threat that
474 escapees pose. According to Jónsdóttir et al. (2018), the genetic diversity of wild lumpfish
475 along the Norwegian coast is so low that if individuals translocated within the country escape
476 from aquaculture stations, they would probably have little to no impact on the genetic
477 composition of the local fish populations. However, this low genetic diversity makes these
478 local populations vulnerable to genetic introgression from other populations (Whittaker et al.,

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479 2018). Considering the exponential increase in demand for lumpfish in the last decade,
480 translocation of individuals from non-Norwegian populations likely will occur in the near
481 future. This scenario poses an additional threat to wild lumpfish populations that are already
482 overexploited due to capture of mature wild individuals for use as broodstock and at risk of
483 diseases spread by escapees from salmon farms (Powell et al., 2018a).

484 Salmon farmers need to consider multiple factors when choosing lumpfish sizes to use in
485 their cages, including the interaction with other species in the cages, delousing efficiency, and
486 rearing cost. Our results highlight the importance of also considering potential changes in
487 mesh state (i.e., how exposed the netting is to sea state and currents) and the morphological
488 properties of lumpfish when determining the minimum sizes of fish to be used. Finally, the
489 results presented here can be used to develop new guidelines for scientists and the industry
490 that will contribute to reducing the escape risk of lumpfish from salmonid farms and the
491 consequent potential environmental issues posed by escapees.

492

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499

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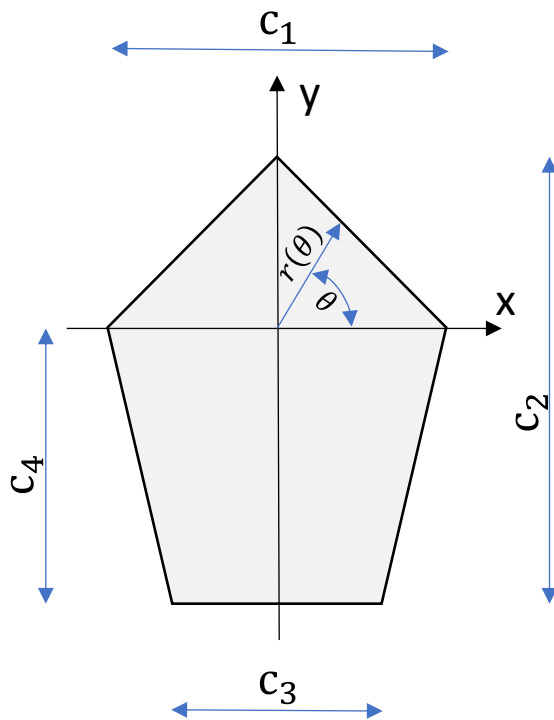
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630

631 Appendix

632 This appendix contains a description of the penta model considered to describe the cross-
633 section shape of lumpfish. The penta model is defined by the two widths c_1 and c_3 together
634 with the two heights c_2 and c_4 (Fig. A1).



635

636 FIG A1: Description of the penta shape model and its parameters.

637 The description in polar coordinates (θ, r) of the penta shape becomes:

$$638 \quad r(\theta) = \begin{cases} \frac{c_2 - c_4}{\sin(\theta)} + 2 \times \frac{c_2 - c_4}{c_1} \times \cos(\theta); \forall \theta \in \left[0.0; \frac{\pi}{2}\right] \\ \frac{c_2 - c_4}{\sin(\theta)} - 2 \times \frac{c_2 - c_4}{c_1} \times \cos(\theta); \forall \theta \in \left[\frac{\pi}{2}; \pi\right] \\ -\frac{c_1 \times c_4}{(c_1 - c_3) \times \sin(\theta)} + 2.0 \times \frac{c_4}{c_1 - c_3} \times \cos(\theta); \forall \theta \in]\pi; \varphi_1] \\ -\frac{c_4}{\sin(\theta)}; \forall \theta \in]\varphi_1; \varphi_2] \\ -\frac{c_1 \times c_4}{(c_1 - c_3) \times \sin(\theta)} - 2.0 \times \frac{c_4}{c_1 - c_3} \times \cos(\theta); \forall \theta \in]\varphi_2; 2\pi] \end{cases}$$

639 where

$$640 \quad \varphi_1 = \tan^{-1}\left(\frac{-c_4}{-0.5 \times c_3}\right)$$

$$641 \quad \varphi_2 = \tan^{-1}\left(\frac{-c_4}{0.5 \times c_3}\right)$$

Declaration of interests

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

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Bent Herrmann: Conceptualization, Methodology, Software, Validation, Formal Analysis, Investigation, Data curation, Writing – Original Draft –Review & Editing, Visualization.

Manu Sistiaga: Conceptualization, Methodology, Validation, Formal Analysis, Investigation, Data curation, Writing – Original Draft –Review & Editing, Visualization, Project administration, Funding acquisition.

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