

The effect of aggregation on visibility in open water

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Abstract

Aggregation is a common life-history trait in open-water taxa. Qualitative understanding of how aggregation by prey influences their encounter rates with predators is critical for understanding pelagic predator-prey interactions and trophic webs. We extend a recently-developed theory on underwater visibility to predict the consequences of grouping in open water species in terms of increased visual detection of groups by predators. Our model suggests that enhanced visibility will be relatively modest, with maximum detection distance typically only doubling for a 100-fold increase in the number of prey in a group. This result suggests that although larger groups are more easily detected, this cost to aggregation will in many cases be dominated by benefits, especially through risk dilution in situations where predators cannot consume all members of a discovered group. This in turn helps to explain the ubiquity of grouping across a great variety of open-water taxa.

Keywords: grouping, anti-predator defence, shoal, school, dilution of risk, attack abatement

Introduction

Aggregation is a dominant feature of the life-histories of many organisms (e.g. flocks of birds, shoals of fish, herds of ungulates, clusters of insect eggs). Of the many selective benefits that group living can confer, those related to reducing predation risk (e.g. through collective vigilance, collective defence, predator confusion, and risk dilution) seem the most ubiquitous (see [1] and [2] for reviews). However, these benefits to group living will be moderated or even nullified if predators (and other antagonists – such as parasitoids) can detect groups at greater distances than they can detect single individuals. There is a paucity of current theory and empirical exploration related to the ability of predators to detect groups of prey, and how that might be affected by different traits of that group. This is a significant handicap to understanding the ecological consequences stemming from aggregation as a widespread anti-predatory defence. Firstly, aggregation plays a facilitating role in human harvesting of natural populations; with many species targeted only because their tendency to aggregate makes harvesting economically viable [3]. Secondly, as species introductions, range-changes and extinctions alter ecosystems, our ability to predict consequences will critically depend on our understanding of interspecific interactions (especially predation – given its ubiquity). Finally, the detectability of aggregations is also important in ecological contexts other than predator-prey or host-parasite interactions. For example pollinators are attracted to larger aggregations of flowers from a greater distance away, and this has been linked to increased detectability (e.g. [4 & 5]). A similar effect has also been reported for attraction of seed-dispersers to aggregations of fruits (e.g. [6]). An improved quantitative understanding of how aggregation affects visual detection is vital in these contexts too.

Existing theory on visual detection of groups of targets

51 The most commonly cited theory on the issue of group visibility remains that of Vine
52 [7,8]. Vine [7] considered a tightly packed chain of n individuals, each of width l and height h ,
53 which form a straight line of length nl and height h when viewed from the side. He argued that
54 in terms of visual acuity the important dimension is the minimum one (h in this case), and thus
55 the length of the line formed by the n individuals was irrelevant to its ease of detection, and
56 detection rate would be independent of group size. In Vine [8], he admitted that a body of
57 evidence existed suggesting that humans could more easily detect horizontal lines than points
58 of the same height. He thus revised his argument to suggest that the maximum distance (r) at
59 which a chain of individuals could be detected would take the form

60

$$61 \quad r = A \left(\frac{nl}{h} \right)^B$$

62

63 where A and B were empirically-determined constants. He suggested on the basis of
64 experiments with human observers that B seemed to be of the order 0.40-0.45. A consequence
65 of these values is that r initially rises steeply (r doubling as n increases from 1 to 5), but this
66 effect quickly wanes in strength at larger group sizes (with highly reduced differences in r
67 above $n = 50$). Vine pointed out that the consequences of having less packed individuals so that
68 there are gaps in the viewed aggregation were unknown, and this remains true. To this we
69 would add that the contrast of individuals with the background will strongly influence
70 detectability and is unexplored in this theory. Further, the ecological applicability of this work
71 is limited, since only a small fraction of natural aggregations involve long chains of
72 individuals.

73

74

75

Turner & Pitcher [9] provided the most influential theoretical work for the overall
effect of aggregation on not just detection but prey capture rates. Their theory explored two
simple alternative assumptions for the effect of group size on detection rates: assuming that the

76 probability per unit time of a group of prey being detected by a nearby predator is either
77 independent of group size (n), or increases linearly with n . The authors argued that these two
78 alternatives likely bracket reality for most natural systems. However, the distribution of real-
79 world cases within this very wide bracket remains unclear. Ioannou et al. [10] argued that
80 detectability of a group should increase with the visual angle subtended by the group.
81 However, they did not speculate on how increasing visual angle will translate theoretically into
82 ecologically-relevant measures such as rate of detection. Treisman [11], on the basis of
83 unpublished experiments with humans, argued that the probability of target detection increases
84 linearly with increasing angular area of the target until a critical area is reached, after which
85 further increasing area brings no further improvement.

86

87 *Motivation for our work*

88 Modelling vision is considerably more tractable in pelagic environments than other
89 habitats; because the background against which objects are viewed is simple and predictable,
90 and detection range is strongly influenced by well-characterised patterns of absorption and
91 scattering of light. Hence, there have been a number of theoretical predictions of pelagic visual
92 detection (e.g. [12-14] and references therein). However, no previous study has explicitly
93 explored the detection of a group of individuals. Recently Nilsson et al. [15,16] have offered a
94 general theory for the visual detection of objects in this environment. Here we build on that
95 framework, extending it to the situation where an approximately spherical group of targets
96 (such as a tightly packed school of fish called a bait ball) is detected visually by something
97 with a camera eye (e.g. a cetacean or predatory fish) viewing it horizontally.

98 An understanding of the anti-predatory effectiveness of grouping is particularly
99 important in the pelagic realm, the largest habitat on the planet. Grouping is a common life-
100 history trait in this environment. With no physical structures to offer protection, prey

101 aggregation is an important and common anti-predatory strategy. The consequences of
102 aggregation for rates of discovery by predators are critical for understanding pelagic predator-
103 prey interactions, and trophic webs. In the next section we develop a new theory for the effects
104 of group size and various ecological factors on maximum detection distance in an open-water
105 environment. A key part of this theory is the attenuation of light as it passes through water,
106 which is substantially greater than in air. Thus the application of our theory is currently limited
107 to aquatic systems, although it could be adapted to terrestrial and aerial situations where the
108 background against which prey are viewed is relatively simple (e.g. snowfields, the sky,
109 mudflats).

110

111 **Methods**

112 *General theory*

113 We model detection of a compact spherical school of fish (henceforth called a bait
114 ball). We begin with the following definitions:

115

116 N_t number of photons collected by the retina in one integration time from the target bait
117 ball at a negligible viewing distance. We assume that the eye employs spatial
118 summation to collect all photons from the ball in one big ‘pixel’. This is known as
119 optimal summation [16], which maximizes detection range, and thus provides an upper
120 bound for the effect of aggregation on visibility.

121

122 N_b number of photons from the background water (over a pixel the same angular size as
123 the bait ball pixel)

124

125 N_p number of photons scattered into the path between the viewer and the bait ball as
 126 viewing distance increases. This is typically referred to as ‘pathlight’.
 127
 128 C_0 inherent Weber contrast of the bait ball against the background water. Given by $N_t/N_b -$
 129 1. For simplicity, we assume that the bait ball consists of enough individuals that it
 130 appears as a solid wall of opaque fish. Thus the contrast of the ball equals the contrast
 131 of the individual fish. This contrast attenuates with distance r following
 132 $C = C_0 e^{(K \cos \theta - c)r}$, where c and K are the beam and diffuse attenuation coefficients of the
 133 water, and θ is the viewing angle of the predator (0° for looking directly upwards, 180°
 134 for looking directly downwards) [17].

135

136 The pelagic light field is approximately monochromatic at viewing angles greater than
 137 48° from vertical (i.e. outside Snell’s window) even at relatively shallow depths below the
 138 surface, and at all viewing angles at depths greater than approximately 100 m [18]. In these
 139 situations, the beam and diffuse attenuation coefficients of the water (c and K) can be
 140 considered to be approximately constant and equal to the values at the wavelength of peak
 141 penetration (480 nm in this study). In this case, the four terms defined above are related as:

142

$$143 \quad N_t = N_b (C_0 + 1) e^{(K \cos \theta - c)r}, \text{ and } N_p = N_b (1 - e^{(K \cos \theta - c)r}) \quad (1) \text{ and } (2)$$

144

145 The first part of (1) is obtained from solving the Weber contrast equation; the second
 146 (exponential) part is obtained from the contrast attenuation equation given above. Equation (2)
 147 is from the pathlight equation for horizontal viewing [17,19]. Now, from [16]:

148

149 $|N_t + N_p - N_b| = R\sqrt{N_t + N_p + N_b}$ (3)

150

151 at the maximum sighting distance, where R is the reliability coefficient. The photoreceptor
 152 noise term introduced by Nilsson et al. [16] is negligible at the euphotic depths examined in
 153 this study (<200 m) and thus excluded. Substituting (1) and (2) into (3) gives:

154

155 $N_b |(C_0 + 1)e^{(K \cos \theta - c)r} + (1 - e^{(K \cos \theta - c)r}) - 1| = R\sqrt{N_b [(C_0 + 1)e^{(K \cos \theta - c)r} + (1 - e^{(K \cos \theta - c)r}) + 1]}$ (4)

156

157 Combining terms gives:

158

159 $\sqrt{N_b} |C_0| e^{(K \cos \theta - c)r} = R\sqrt{C_0 e^{(K \cos \theta - c)r} + 2}$ (5)

160

161 As mentioned above, $C_0 e^{(K \cos \theta - c)r}$ is the apparent contrast of the bait ball at viewing distance r
 162 and thus is much less than two at the sighting distance unless the light levels are extremely
 163 low, so (5) is well approximated as:

164

165 $\sqrt{N_b} |C_0| e^{(K \cos \theta - c)r} \cong R\sqrt{2}$ (6)

166

167 From [16]:

168

169 $N_b = \frac{\pi}{4} \left(\frac{T}{r}\right)^2 \left(\frac{\pi A^2}{4}\right) q\tau\Delta t \int_{\lambda_1}^{\lambda_2} (1 - e^{-kR(\lambda)l}) L_b(\lambda) d\lambda$ (7)

170

171 where T is diameter of the bait ball. For the viewing organism A , q , τ , and Δt are the diameter
 172 of the pupil, the quantum efficiency of the photoreceptors, the ocular transmittance, and the
 173 integration time of the photoreceptors respectively. The parameters k and l are the absorption
 174 coefficient and the length of the photoreceptors respectively. $L_b(\lambda)$ is the spectral radiance of
 175 the background light and $R(\lambda)$ is the normalized absorbance spectrum of the photoreceptors.

176 We define:

177

$$178 \quad N_0 = \left(\frac{\pi A^2}{4} \right) q \tau \Delta t \int_{\lambda_1}^{\lambda_2} \left(1 - e^{-kR(\lambda)l} \right) L_b(\lambda) d\lambda \quad (8)$$

179

180 which is the number of photons absorbed by a pixel that views a region one steradian in
 181 angular area. This can be thought of as the product of the sensitivity of the eye and the amount
 182 of light available for vision. Since the terms can not be separated, due to the weighted integral,
 183 they are considered as one. Substituting equation (8) into equation (5) gives:

184

$$185 \quad \sqrt{\frac{\pi}{4}} \frac{T}{r} \sqrt{N_0} |C_0| e^{(K \cos \theta - c)r} \cong R\sqrt{2} \quad (9)$$

186

187 Now T , which is the diameter of the spherical bait ball, is related to the number of fish in the
 188 target group n via:

189

$$190 \quad T = \sqrt[3]{\frac{6nV_0}{\pi}} \quad (10)$$

191

192 where V_0 is the volume each fish occupies in the bait ball (including the fish and the
 193 surrounding water). This volume varies by species and swimming speed, but is approximately

194 the cube of the body length of the fish for a school larger than 50 individuals [20]. Substituting
 195 (10) into (9) and rearranging gives:

196

$$197 \quad r e^{(c-K \cos \theta)r} \cong \frac{|C_0|}{R} \sqrt{\frac{\pi}{8}} \sqrt{N_0} \sqrt[3]{\frac{6nV_0}{\pi}} \quad (10)$$

198

199 Gathering the constants and setting the reliability coefficient R to 1.96 (the value for 95%
 200 confidence of detection), we get:

201

$$202 \quad r e^{(c-K \cos \theta)r} \cong 0.4 |C_0| \sqrt{N_0} \sqrt[3]{nV_0} \quad (11a)$$

203

204 which can be solved for r as:

205

$$206 \quad r \cong \frac{W \left[0.4(c - K \cos \theta) |C_0| \sqrt{N_0} \sqrt[3]{nV_0} \right]}{c - K \cos \theta} \text{ or} \quad (11b)$$

207

$$208 \quad r \cong \frac{1}{c} W \left(0.4c |C_0| \sqrt{N_0} \sqrt[3]{nV_0} \right) \quad (11c)$$

209

210 for horizontal viewing. $W(x)$ is the LambertW function (the inverse of $y = xe^x$), which can be
 211 calculated using Matlab, Maple, Mathematica and other computational packages.

212

213 *Specific example parameter values*

214 For the visual system of an Atlantic blue marlin predator (*Makaira nigricans*),
 215 representative values are: pupil diameter $A = 0.019$ m, integration time $\Delta t = 0.017$ s, ocular
 216 transmittance $\tau = 0.8$, and quantum efficiency $q = 0.34$. The photoreceptors of the marlin have

217 a peak absorbance at 480 nm, an absorption coefficient of $0.035 \mu\text{m}^{-1}$, and a length of 57 μm
218 [21].

219

220 The background radiance spectra ($L_b(\lambda)$) were modeled using measured profiles of
221 inherent optical properties and commercial radiative transfer software (HydroLight 5.1,
222 Sequoia Scientific). The ability of radiative transfer theory to accurately model oceanic
223 radiance distributions has been validated by *in situ* measurements of selected radiances and
224 irradiances in multiple studies (e.g. [22][23]). The agreement between modeled and measured
225 spectral radiances is particularly good in oceanic waters, which are easily characterized
226 (reviewed by [18]).

227 Depth profiles of inherent optical properties and chlorophyll-a concentration from
228 tropical oceanic water (approximately Jerlov oceanic type I; [24]) needed for the radiative
229 transfer software were obtained from Drs. Andrew Barnard, Scott Pegau and Ronald Zaneveld
230 (College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, Oregon),
231 who collected them using a dual path, multiband absorption and attenuation meter (ac-9,
232 WETLabs) and fluorometer in the Equatorial Pacific ($0^{\circ}0'N$ $177^{\circ}21'W$). Absorption and
233 beam attenuation coefficients (at 412, 440, 488, 510, 532, 555, 650, and 676 nm) were
234 measured to a depth of 199 m and chlorophyll-a concentration was measured at 1 m intervals
235 to a depth of 110 m (Figure 1a).

236 Underwater radiance distributions were calculated from 400 to 700 nm at 10 nm
237 intervals and the surface to 200 m depth at 10 m intervals. The sky was assumed to be
238 cloudless, the sea to be calm, and the sun at the zenith. The sky irradiance was calculated
239 using the Radtran model ([25]), and the sky radiance angular distribution was calculated using
240 the semi-empirical model given in [26]. Both models account for atmospheric effects, such as
241 the reddening of the sun as it approaches the horizon, and are well established. Pure water

242 absorption was taken from [27] , and the particle scattering phase function was an average-
243 particle phase function based on measurements by Petzold [28]; tabulated values are given by
244 Mobley [18, table 3.10]. Chlorophyll fluorescence was calculated from the measured
245 chlorophyll-a concentration using a modeled phytoplankton absorption spectrum taken from
246 [29] and a fluorescence efficiency of 0.02 that was independent of excitation wavelength.
247 Raman scattering by the water molecules was also included [30]. These values were used to
248 calculate estimates of the number of photons captured per steradian per integration time (N_o).
249 Figure 1b shows the values for three oceanic predators as a function of depth.

250

251

252 **Results**

253

254 In figure 2 we plot maximum horizontal sighting distance (r) as a function of the
255 number of fish in the group (n , varying over three orders of magnitude from 10 to 10,000) and
256 depth (from 0 at the surface to 200 m depth) for three values of the inherent Weber contrast
257 between the fish and the background (0.25, 0.5 and 1). For reference, a contrast of 0.25 would
258 be found in a relatively cryptic silvery fish, such as a herring or sardine, a value of 0.5 would
259 be for a typical reef fish, and a value of one would be for a black fish. We solve equation (11)
260 for the maximum distance (r) at which the group of individuals of approximate individual
261 lengths of 10 cm can be detected. Our key results are however qualitatively unchanged for
262 different sized fish. For example, by inspection of equations (9) and (11), we can see
263 (unsurprisingly) that we predict that larger individual size of fish leads to longer sighting
264 distances, but this effect is relatively modest, with the rate of increase being much slower than
265 linear.

266 Our first key prediction concerns the inherent visual contrast of the prey against the
267 background. It is unsurprising that r increases with increasing inherent contrast (C_0) of the
268 prey. What is less obvious is that this effect is non-linear: having a four times greater contrast
269 does not increase sighting distance four-fold. This is because sighting distance is related to a
270 function of the natural logarithm of the contrast (the effect of change in contrast can be seen in
271 greatest detail in Figure 3). Also less obvious is that there is no strong effect of contrast on the
272 shape of the r - n relationship, and so we would not expect the visibility costs of grouping to be
273 inherently different for prey of different contrasts against the background. By inspection of
274 equation 11, all three terms on the right will be the same in this regard: inherent contrast, the
275 square root of photons (the weighted product of the intensity of illumination and sensitivity of
276 the viewer), and the cube root of the bait ball volume (and so the length of the individual prey
277 fish) all affect the relative sighting distance in a similar way. As a rule of thumb, the number
278 of photons drops by a factor of ten every 70 m in clear oceanic water [18], so the square root
279 drops by a factor of about three. Thus, as an example, cutting contrast to a third of what it was
280 has the same effect as moving the bait ball 70 m deeper or cutting the number of individuals by
281 a factor of 27. This line of arguments may explain why schooling pelagic fish nearly always
282 invest in mirrored scales that reflect much of the incident light to drop their inherent contrast
283 considerably [31].

284 Our next key result is the effect of depth, with sighting distances being maximised at
285 around 100m, above that the dominant factor is higher attenuation of horizontally travelling
286 light (high c) caused by suspended particles (e.g. phytoplankton), and below that the dominant
287 factor is low incident light levels (leading to low N_0) caused by attenuation of sunlight as it
288 passes through the surface waters above.

289 Our primary interest has been in predicting the relationship between maximum sighting
290 distance (r) and group number (n). Unsurprisingly, r increases with n under all circumstances.

291 It is also perhaps unsurprising that the r - n relationship flattens as n increases, but what is less
292 obvious is that (even over the broad range of n considered) there is no saturation of the curve.
293 That is, we can still see appreciable increase in r as n changes from 1,000 to 10,000 for
294 example. This is due to optimal summation, which allows the fish to make its visual pixel the
295 same size as the bait ball. Thus, at least over the situations we model, there is no ceiling effect
296 whereby after a group reaches a certain size, further increases in size do not increase the ease
297 of detection of the group. However of most interest is the relatively modest effect of
298 increasing n : under all the circumstances that we explored, increasing the group size by two
299 orders of magnitude (i.e. multiplying n by a factor of 100) causes r to rise by less than a factor
300 of two. Even this is likely an over-estimate, since not all animals employ optimal summation.
301 By assuming optimal summation we are finding the longest possible sighting range. The
302 relatively modest costs of grouping in terms of increased visual detection may be relatively
303 easily outweighed by benefits through risk dilution, collective vigilance and/or confusion
304 effects, all of which have been demonstrated to increase rapidly with increasing group size (see
305 Discussion and [1]). If maximum sighting distance doubles, then this would suggest that the
306 volume of space over which the prey can be detected increases by a factor of eight. Thus, our
307 model predicts that (as would be expected) a group of 5,000 pelagic prey is more obvious to
308 predators than a group of 50, and this should increase the rate at which the larger group is
309 discovered by predators, but only by a factor of eight or less, the exact number depending on
310 the details of the predator's foraging strategy.

311 In Figure 3, we show a greater range of values of contrast for three levels of N_0 ,
312 corresponding (for our Blue Marlin viewer) to depths of about 50, 100 and 200 m (beam
313 attenuation coefficient c is considered to be at a constant value of 0.1 for all three situations).
314 This emphasizes that the inevitable rise in sighting distance with increasing group size can be
315 counteracted by a decrease in the inherent contrast, leading to our prediction that the larger the

316 characteristic shoal size of fish the stronger the selection pressure should be for morphological
317 adaptations (most obviously mirrored scales) that reduce contrast.

318 It is important to note that our visual model allows the minimum contrast threshold of
319 the viewer to go well below levels that have actually been measured. It may very well be that
320 natural predators do achieve these low levels, but so far this has not been demonstrated in large
321 pelagic predators. The lowest threshold measured for fish (and indeed for any animal) is 0.005
322 [32]. Figure 4 shows the sighting distance versus depth and group size using the same
323 procedures as used to generate Figure 2 but with the additional constraint that the contrast
324 threshold of the viewer cannot go below 0.005. As can be seen by comparing Figures 2 and 4,
325 this added constraint does not change any of our qualitative conclusions. Interestingly though,
326 group size does not affect sighting distance at all at shallower depths under this constraint. For
327 the viewer to get any advantage when viewing larger groups at these depths, its contrast
328 threshold would have to be very low indeed. One thing that is obvious from both figures 2 and
329 4 is that water clarity has the biggest influence on sighting distance, because it is the only
330 variable outside the (very slowly increasing) LambertW function. This is why the schools can
331 be seen at greater distance at depth despite it being darker, so long as the water is clearer, an
332 effect commonly experienced by scuba divers as they drop below the murky surface layer to
333 the darker but clearer depths.

334

335 Discussion

336

337 The main prediction of our model is that in general a 100-fold increase in the number of
338 individuals in a group will only lead to at most a doubling in the range at which prey are visible
339 to a predator and so (in a worst case where individuals could be detected from all angles) the

340 larger group might be detected eight times as frequently as the smaller. We now consider the
341 anti-predatory benefits of grouping for comparative purposes.

342 The benefits of risk dilution can sometimes be substantial. If the predator is relatively
343 small in comparison to the prey and not as fleet as the prey, then it may only be able to capture
344 a single individual from a group. In this case, the dilution benefits of being in a group a
345 hundred times larger (and having the risk of being the selected individual reduced by a factor
346 of 100) will far outweigh the eight-fold increase in frequency of encounter of the group with a
347 predator. However at the opposite extreme where the predator is large (or hunts in packs) and
348 fleet compared to the prey, then all of a discovered group may be consumed and there is no
349 dilution benefit to grouping. In general, available empirical evidence (reviewed in [2]) suggests
350 both these extreme situations are commonplace, and ecologically and taxonomically
351 widespread. We can conclude that in cases where a single attack captures only a single
352 individual or small fraction of the prey group, and a predator cannot repeatedly attack a
353 discovered group, then dilution benefits will exceed the visibility costs estimated here.

354 Although predator confusion resulting in a reduced ability to capture prey when faced
355 with larger moving groups has often been demonstrated (see Beauchamp [2] for a review) the
356 effect of group size has rarely been quantified, and current theory does not allow strength of
357 confusion and prey survival to be quantitatively linked [33] . However the confusion effect can
358 be strong. In the most thorough study of the effects of group size, Landeau & Terborgh [34]
359 demonstrated that predatory bass were always successful in quickly capturing a single minnow
360 when both were in an experimental arena together. In contrast, this success rate (for capturing
361 every single minnow) dropped to 11% despite an extended time for interaction when the prey
362 group size was increased to 15. Our model suggests that such an effect could again dominate
363 the cost of increased ease of detection of larger groups.

364 If we turn to increased vigilance as another anti-predatory benefit of grouping, the most
365 relevant data from the recent extensive review of Beauchamp [2] is that of Kenward [35] on
366 the characteristic distance at which flocks of woodpigeons reacted to apparent attacks by a
367 trained goshawk. Single pigeons reacted on average when the goshawk was only 4m away, this
368 distance increased four-fold for flocks of between two and ten birds and ten-fold for flocks of
369 more than fifty. Interpretation of such data is complicated because there may be a lag between
370 detection of the approaching predator and flight response, but this is likely to be low in this
371 system where predators are much more successful if they can pin prey to the ground, and in
372 any case such a lag is likely to be bigger for large flocks where risk dilution will be substantial.
373 However, as with confusion, it is difficult to quantify the relationship between early predator
374 detection and prey survival. Clearly there is a dearth of data quantifying how vigilance benefits
375 of aggregation change with aggregation size, but given the modest costs of increased detection
376 estimated here there is at the very least no reason to reject the possibility of vigilance benefits
377 outstripping these costs. However, vigilance for predators is particularly beneficial in situations
378 where forewarned prey can flee to a place of safety, and this option is generally not available in
379 pelagic environments.

380 Finally, another factor that mitigates the cost of larger groups being detectable at a
381 greater distance is that, for finite prey populations, increases in group size correspond with a
382 decrease in the total number of groups in the environment. This reduction in the density of
383 groups means at any one time a predator will be a greater distance on average from the nearest
384 group [9,10]. However, evaluation of the consequences of this for predators and prey would
385 require consideration of how such aggregation changed not just average distance from prey but
386 also predator activity budgets and search strategies (i.e. in terms of speed and direction of
387 travel during searching). This is an open but tractable problem theoretically, which (in common

388 with all work on predation) should benefit from a step change in our ability to collect data on
389 free-living animals through miniaturisation of on-board data-loggers [36]
390 Finally, we also note that the benefits of remaining in a group often appear to hold across a
391 broad range of group sizes, and after attack on the group has begun. Observation of bait balls
392 suggests that the tenancy to aggregate remains even as the ball of fish is whittled away by a
393 group of predators [37].

394

395 In summary, we have been able to offer an estimate of the likely consequences of
396 grouping in open water species in terms of increased visibility of groups to predators. Our
397 model suggests that such enhanced visibility will be relatively modest, with maximum
398 detection distance only doubling for a 100-fold increase in the number of individuals in the
399 group. This suggests that although larger groups will likely be detected and attacked more
400 often by predators, cost to grouping will in many cases be dominated by benefits through
401 (some or all of) risk dilution, predator confusion, and enhanced collective detection of
402 approaching predators. This helps to explain the ubiquity of grouping across a great variety of
403 open-water taxa – the greatest predation cost to this behaviour is likely to be dominated by
404 expected benefits.

405

406 **Acknowledgement**

407 We thank Eleanor Caves, Julia Notar, Sarah Solie, and Kate Thomas; Drs. Nicholas Brandley,
408 Robert Fitak, Daniel Speiser, and Eric Warrant; and two anonymous reviewers for valuable
409 comments.

410

411

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486

487 **Figure Captions**

488

489 **Figure 1:** The optical parameters in the water studied.) A) The beam attenuation coefficient
490 (at 480 nm) as a function of depth. B) The number of photons (on a log scale) absorbed by the
491 eye of an Atlantic Blue Marlin (*Makaira nigricans*: pupil diameter = 0.019 m) in one
492 integration time if looking horizontally and viewing a full steradian in a sample of clear
493 oceanic water (N_0). To show the effect of pupil diameter on N_0 , values for two other pelagic
494 predators – the Atlantic Mackerel (*Scomber Scombrus*: pupil diameter = 0.0096 m) and the
495 Bluefin Tuna (*Thunnus thynnus*: pupil diameter = 0.036 m) – are also given. All visual
496 parameters other than pupil diameter remain that of the marlin.

497 **Figure 2:** Sighting distance (in meters) of a spherical bait ball of fish (each being 0.1 m in
498 length) as a function of depth and number of fish in the ball (on a log scale). The left, middle,
499 and right panels correspond to fish with inherent contrasts of 0.25, 0.5 and 1.0 respectively.
500 The complex effect of depth on sighting distance is due to the fact that deeper water is both
501 darker and clearer, which affect sighting distance in opposite ways.

502 **Figure 3:** Sighting distance (in meters) of a spherical bait ball of fish (each being 0.1 m in
503 length) as a function of both the inherent contrast and number of fish in the ball (on a log
504 scale). The left, middle, and right panels correspond to the number of photons absorbed by a
505 marlin eye (N_0 , see text) at daytime depths in clear oceanic water of approximately 200, 100,
506 and 50 meters respectively (the beam attenuation coefficient $c = 0.1 \text{ m}^{-1}$ throughout).

507

508 **Figure 4:** Sighting distance (in meters) of a spherical bait ball of fish (each being 0.1 m in
509 length) as a function of depth and number of fish in the ball (on a log scale). The left, middle,
510 and right panels correspond to fish with inherent contrasts of 0.25, 0.5 and 1.0 respectively. In

511 this case (as opposed to the results shown in Figure 2), the minimum contrast threshold of the
512 viewer is not allowed to drop below 0.005, which is the lowest value measured in any animal.

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