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1 **Potential for managing life history diversity in a commercially**
2 **exploited intermediate predator, the goldsinny wrasse**
3 **(*Ctenolabrus rupestris*)**

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24 **Abstract**

25 Small-bodied wrasse species are important for structuring coastal marine ecosystems
26 but are also increasingly harvested as parasite cleaners on farmed salmon. Identifying
27 management regulations that will support long-term sustainability of wrasse fisheries is
28 challenging, because there is still limited knowledge about the impacts of fisheries on
29 the demography of these intermediate predators in their natural environments. To this
30 end, we studied individual growth histories of goldsinny wrasse (*Ctenolabrus rupestris*)
31 at a fine spatial scale across replicated marine protected areas (MPAs) and areas open to
32 commercial harvesting on the Norwegian coast. The MPAs were established 1-7 years
33 prior to our sampling. We detected significant fine-scale spatial variation in wrasse
34 asymptotic body size, but found no consistent difference between MPAs and fished
35 areas. Male wrasses reached larger asymptotic body sizes than females, while fyke nets
36 captured individuals with larger asymptotic body sizes compared to baited traps. These
37 are the two commonly used gear types in wrasse fisheries. An extended use of baited
38 traps, along with slot-size limits, could therefore aid in protecting large-growing
39 phenotypes such as nest-guarding males.

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41 **Keywords:** aquaculture, conservation, fisheries, growth, life-histories.

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48 **Introduction**

49 Small-bodied wrasses such as the goldsinny (*Ctenolabrus rupestris*) are increasingly
50 being harvested as cleaner fish for the Northern European aquaculture industry
51 (Skiftesvik *et al.*, 2014). However, these intermediate predators may also play a key role
52 in structuring coastal marine ecosystems, as prey for apex carnivores and predators on
53 planktivorous and benthic herbivores (Moksnes *et al.*, 2008; Baden *et al.*, 2010). In
54 northern European coastal systems, a proposed trophic cascade involves more abundant
55 intermediate predators, such as wrasses, following intense harvesting and depletion of
56 Atlantic cod (*Gadus morhua*) apex predator populations (Fernández-Chacón *et al.*,
57 2015). Wrasses prey on algae-grazing amphipods and isopods, and could thereby
58 influence the state of nearshore seagrass (*Zostera marina*) and seaweed (*Fucus* spp.)
59 ecosystems (Östman *et al.*, 2016).

60 Marine protected areas (MPAs) are to an increasing extent used as a management
61 tool in coastal systems (Fenberg *et al.*, 2012). Specifically, MPAs could help to protect
62 spatial- and behavioural diversity of fish populations as well as a naturally broad
63 composition of age- and size-classes of spawner fish against selective harvesting
64 (Berkeley *et al.*, 2004a; Baskett and Barnett, 2015). In theory, MPAs could also drive
65 reductions in individual growth because of potential crowding effects (e.g., intensified
66 competition for food) when population densities of species protected within MPAs are
67 increasing (Gårdmark *et al.*, 2006). Smaller species may suffer from increased predation
68 when species at higher trophic levels recover within MPAs (Babcock *et al.*, 2010).

69 The goldsinny wrasse (*Ctenolabrus rupestris*) is an abundant intermediate predator
70 distributed in shallow coastal waters of the North-East Atlantic from Morocco to
71 Norway. The species typically prefers rocky- or vegetated substrates with access to

72 refuges such as spaces between rocks, crevices or caves (Costello, 1991; Sayer *et al.*,
73 1993; Gjørseter, 2002a). Goldsinny wrasse may reach 20 years of age and a body length
74 of 18 cm (Darwall *et al.*, 1992; Sayer *et al.*, 1995). The eggs are pelagic and males
75 defend territories up to 2 m² which they may keep for several years (Hilldén, 1981;
76 Sayer, 1999). Commercial exploitation of small-bodied wrasses such as the goldsinny
77 began in the 1990's in Norway and on the British Isles, when it was discovered that
78 their natural behaviour as parasite cleaners on other fish (Potts, 1973) could be used to
79 reduce sea-lice (*Lepeophtheirus salmonis* and *Caligus elongatus*) infestation in
80 salmonid aquaculture (Darwall *et al.*, 1992; Deady *et al.*, 1995; Sundt and Jørstad,
81 1998). Already during the early wrasse fisheries there was concern about the long term
82 sustainability of the fishery, since reductions in the abundance of larger and older fish
83 coincided with the emergence of the fishery (Sayer *et al.*, 1996; Varian *et al.*, 1996).
84 The wrasse catches remained relatively low throughout the 1990's and 2000's, when
85 wrasses were only complementary to chemical treatments. However, more recently, the
86 lice infestation problem in salmonid aquaculture worsened considerably and the annual
87 landings of wild-caught wrasse in Norway have surpassed 20 million individuals
88 (Gonzalez and de Boer, 2017). Wrasses are caught with small vessels using fyke nets
89 and baited pots at shallow depths on rocky, kelp covered habitat (Gjørseter, 2002b;
90 Skiftesvik *et al.*, 2015). Four different species are being harvested in Norway: the
91 goldsinny wrasse, corkwing wrasse (*Symphodus melops*), ballan wrasse (*Labrus*
92 *bergylta*) and rock cook (*Centrolabrus exoletus*). A case study from one Norwegian
93 fjord suggests that corkwing wrasse and goldsinny wrasse hold the larger share of the
94 landings (Skiftesvik *et al.*, 2014, 2015). The official landings statistics from the
95 Norwegian directorate of fisheries confirm this pattern, where goldsinny wrasse and

96 corkwing wrasse each constituted ca. 45 %, followed by ballan wrasse (8 %) and rock
97 cook (2 %) (Gonzalez and de Boer, 2017). In Norway, the first management measures
98 for wrasse were implemented in 2011, introducing a minimum size limit of 11 cm and
99 closure of the fishery during the spring spawning period. However, these regulations
100 have apparently been unsuccessful in protecting mature fish, especially males
101 (Halvorsen *et al.*, 2016).

102 In this study, we explore fine scale spatial variation in life histories of goldsinny
103 wrasse across a network of Norwegian coastal MPAs. Originally, these MPAs were
104 implemented to protect and rebuild depleted populations of European lobster (*Homarus*
105 *gammarus*) and are managed through gear restrictions allowing only hook and line
106 fishing (Moland *et al.*, 2013a). Therefore, the MPAs are not strict no-take marine
107 reserves. However, wrasse fishing for the aquaculture industry is conducted with fixed
108 gear types (fyke nets and baited traps) which are not permitted within the MPAs. Due
109 to its small size, the goldsinny wrasse is not harvested as a food fish by anglers using
110 hook and line (Vølstad *et al.*, 2011). Wrasses are typically sedentary reef fishes with
111 limited home ranges and may therefore benefit from small coastal MPAs (Hilldén,
112 1981; Villegas-Ríos *et al.*, 2013). Indeed, the abundance of wrasse is now generally
113 higher within the Norwegian MPAs than in neighbouring harvested areas (Halvorsen *et*
114 *al.*, 2017a). Albeit relatively small (0.6 – 5.3 km²), the MPAs also offer partial
115 protection to upper-trophic-level predators such as the European lobster and Atlantic
116 cod (*Gadus morhua*), the latter being a potential predator on wrasses (Hop, 1992). On
117 the Norwegian coast, both cod and lobster display sedentary behaviour (Moland *et al.*,
118 2011; Villegas-Ríos *et al.*, 2017) and survival rates and body size have increased within

119 the MPAs for both species (Moland *et al.*, 2013a,b; Fernández-Chacón *et al.*, 2015,
120 2017).

121 We model individual growth trajectories of goldsinny wrasse based on otoliths from
122 scientific samples collected in replicated MPAs and neighbouring harvested areas. A
123 working hypothesis is that the MPAs will protect all phenotypes, including fish that
124 grow to reach a large body size, likely to be correlated with bolder behaviour and
125 selected against in fisheries operating outside the MPAs (Biro and Post, 2008; Réale *et*
126 *al.*, 2010; Biro and Sampson, 2015). Because the MPAs were implemented only in 2006
127 and 2012, we focus on exploring the footprints of ongoing selection (a demographic
128 effect) rather than the long-term consequences of selection (an evolutionary change).
129 Furthermore, we explore how the wrasse fishery could be developed towards a more
130 balanced exploitation regime where population productivity benefits from a natural
131 diversity in life-histories (Schindler *et al.*, 2010; Zhou *et al.*, 2010). We do this by (1)
132 comparing how the two commonly used gear types used in the fishery (fyke nets and
133 baited traps) capture faster versus slower growing life histories, and (2) by sampling
134 across different coastal regions (each holding an MPA) to resolve the spatial scale of
135 life-history structure in this species. Sex is included as a covariate because the territorial
136 behaviour of nesting males could correlate with fast growth trajectories and
137 vulnerability to fishing (Darwall *et al.*, 1992; Halvorsen *et al.*, 2016, 2017b).

138

139 **Material and methods**

140 **Sampling and age determinations**

141 Goldsinny wrasse was sampled within four MPAs and neighbouring control areas open
142 to harvesting along the Norwegian Skagerrak coast from 24 August to 12 September

143 2013 (Figure 1). Two of these MPAs, Flødevigen and Risør, were established in 2006.
144 The two other MPAs included in this study, inner and outer Tvedestrand fjord, were
145 established in 2012 and are managed with the same gear restrictions as the Flødevigen
146 and Risør MPAs. Wrasse were sampled using un-baited fyke nets (diameter: 55 cm,
147 leader: 5 m, mesh size: 30 mm) and two-chamber pots (size: 70 × 40 × 29 cm, entrance
148 diameter 75 mm, mesh size: 15 mm) baited with shrimp (*Pandalus borealis*; for details
149 on sampling effort, see Table 1). The gear was set over night (19-26 hours) at 0-7 m
150 depth on vegetated or rocky substrate. A total of 935 goldsinny was sampled and
151 measured for length and weight. Sex was determined by examining morphology and
152 gonads, while age was determined from sagittal otoliths (Richter and McDermott, 1990;
153 Gordo *et al.*, 2000). For this purpose, whole otoliths were placed in a 96% ethanol bath
154 on a black background, and digital pictures were taken using a Leica microscope (MZ
155 16 A) and camera (DFC425 C) with 20 x magnification. A total of 109 fish were
156 excluded from further analyses because the otoliths were of poor quality and could not
157 be reliably interpreted. For the remaining 826 fish (Table 1), interannual distances
158 (growth zones) were measured along a transect through the horizontal plane of the
159 otolith as the distance from the centre (nucleus) to the outer margin of each opaque
160 annulus, using the open-source image analysis program ImageJ (Abràmhoff *et al.*,
161 2004). Individual otoliths were always read and interpreted by two persons. The age
162 was determined after agreement between both observers. As shown by Sayer *et al.*
163 (1995), we found that the sagittal otoliths were characterised by a white opaque nucleus
164 followed by distinctive alternate transparent and opaque zones (Figure 2), which made
165 age- and growth estimation fairly straight-forward. The Dahl-Lea equation was used for

166 back- calculation of lengths-at-age based on the distances measured on the otoliths

167 (Francis, 1990):

168

$$169 \quad L_a = (O_a / O_c) L_c,$$

170

171 where L_a is the estimated length-at-age a , L_c the length at capture, O_a the distance from

172 the centre of the otolith to the outer edge of the annulus defining age a , and O_c the

173 distance from the centre to the outer margin of the otolith.

174

175 **Growth analyses and statistical modelling**

176 Growth trajectories were back-calculated using von Bertalanffy (VB) growth curves:

177

$$178 \quad L(t) = L_\infty - (L_\infty - L_0)e^{-kt},$$

179

180 where $L(t)$ is fish length at age t , L_∞ the asymptotic length, L_0 the average length at t

181 = 0, and k the intrinsic growth rate (von Bertalanffy, 1938). Non-linear least squared

182 regression, with L_0 , L_∞ and k as free model parameters, was used to fit VB curves to the

183 individual back-calculated growth trajectories (Pardo *et al.*, 2013). Only fish with an

184 otolith age of four years or older were included in these analyses ($n = 413$), since VB

185 curves could not be reliably fit to three data points (back-calculated lengths at age) or

186 less. Linear models, fitted in the statistical software package R using a Gaussian error

187 distribution (R Development Core Team, 2012), were used to investigate effects of

188 MPAs, sex and gear type (as factors) on growth trajectories. We focussed the analyses

189 on L_∞ as the key parameter capturing growth differences as it is strongly and negatively

190 correlated with k (Charnov 1993). Region was included as a factor in the model (four
191 levels: Flødevigen, inner Tvedestrand fjord, outer Tvedestrand fjord, and Risør). We
192 hypothesised that potential effects of MPA treatment and sex on goldsinny wrasse
193 growth trajectories could depend on the sampling region, and thus included two-way
194 interaction terms between these factors in the starting model (Table 2). We also
195 hypothesised that an effect of gear type could depend on sex, perhaps due to
196 behavioural differences, and therefore included this interaction effect in the starting
197 model as well (Table 2). Prior to model selection data were explored following the
198 protocol described by Zuur *et al.* (2010; see also, Zuur *et al.*, 2016). One outlier with an
199 estimated asymptotic length of 710 mm was excluded from further analyses. The
200 response variable (L_{∞}) was log-transformed to improve normality. A residual plot
201 indicated that our starting model, including all relevant factors and interaction effects,
202 fitted the data adequately and thus provided a good starting point for model selection
203 (Supplementary material). The Akaike information criteria AIC was used for model
204 selection, where the model having the lowest AIC value was considered the most
205 parsimonious one and used for inference (Burnham and Anderson, 1998). We
206 acknowledge that some uncertainty in the response variable, associated with the fitting
207 of VB growth curves, will not be accounted for in the linear model. However, the VB
208 curves closely fitted the back-calculated lengths (see Results). Also, by focussing the
209 analyses on fish that were at least four years old, our results will not be biased by
210 incomplete juvenile growth curves with potentially greater uncertainty in parameter
211 estimates.

212

213 **Results**

214 The otoliths revealed considerable variation in back-calculated growth trajectories of
215 goldsinny wrasse (Figure 2). The fastest growing fish were approximately 100% larger
216 at age compared to the slowest growing fish (Figure 2). VB curves closely fitted to the
217 back-calculated growth trajectories; R^2 ranged between 97.9 and 100%. The most
218 parsimonious linear model supported a two-way interaction effect between sex and gear
219 type, as well as between MPA treatment and region, on asymptotic length (Table 2,
220 Table 3). This model, on which we based inference about variation in goldsinny wrasse
221 asymptotic lengths, had an AIC value 1.7 units below the second best model that also
222 included a two-way interaction effect between sex and region (Table 2). Excluding the
223 interaction effect between sex and gear type from the best model increased the AIC by
224 2.6 units. Thus, the data provided fairly strong support for this interaction effect on
225 wrasse growth histories. Overall, male goldsinny wrasse reached larger asymptotic
226 lengths compared to females, while the baited traps captured goldsinny wrasse with
227 smaller asymptotic lengths than the fyke nets (Figure 4). The difference in asymptotic
228 length between sexes was significantly larger for baited traps compared to fyke nets (i.e.
229 the interaction effect, Figure 4). Excluding the interaction effect between MPA
230 treatment and region from the best model increased the AIC by 61.1 units. Thus, the
231 data provided very strong support for this interaction effect, showing that there was no
232 consistent difference in asymptotic length between MPAs and control areas across the
233 four regions. Compared to neighbouring harvested areas (controls), asymptotic lengths
234 were larger in the Flødevigen MPA and the MPA from the outer Tvedestrand fjord,
235 while the opposite pattern was seen in the Risør region and the inner Tvedestrand fjord
236 (Figure 5). Overall, asymptotic lengths were smallest in the MPA from the inner
237 Tvedestrand fjord and largest in the control area in Risør (Figure 5).

238

239 **Discussion**

240 This study from the Norwegian coast revealed that growth histories of goldsinny wrasse
241 can differ considerably at a spatial scale of five km or less. Our data did not, however,
242 support a consistently positive effect of coastal MPAs on the asymptotic body size of
243 this intermediate predator. Outside the MPAs, the goldsinny wrasse is increasingly
244 harvested as a cleaner fish for the aquaculture industry. By comparing the two gear
245 types commonly used in this fishery, our study showed that baited traps tend to capture
246 fish characterised by smaller asymptotic body sizes compared to those captured in
247 unbaited fyke nets. Overall, male goldsinny wrasse also grew to reach larger asymptotic
248 body sizes compared to females. These findings may guide future management of the
249 wrasse fishery.

250 Our working hypothesis was that the MPAs would protect fish that grow to reach a
251 large body size, a life history which is often correlated with bold behaviour and selected
252 against in fisheries (Swain *et al.*, 2007; Uusi-Heikkilä *et al.*, 2015; Alós *et al.*, 2016;
253 Klefoth *et al.*, 2017). Data from the Flødevigen region and the outer Tvedestrand region
254 provided some support for this hypothesis. Here, the estimated asymptotic body size
255 was larger inside the MPA compared to the neighbouring fished area. However, data
256 from the two other study regions, Risør and the inner Tvedestrand fjord, showed an
257 opposite pattern. We note that the MPAs included in this study are still young
258 (established 1-7 y before our sampling took place) relative to the potential life span of
259 the goldsinny wrasse, which is about 20 y (Darwall *et al.*, 1992). Thus, the demographic
260 footprints of ongoing protection from fishing might not yet be fully realised. That said,
261 there was no consistent difference between older and younger MPAs, since a positive

262 effect was seen in one of the old MPAs (Flødevigen) as well as one of the young MPAs
263 (outer Tvedestrand).

264 Unfortunatley, we lack robust estimates of other biotic and abiotic environmental
265 factors that could potentially explain the observed fine-scale spatial variation in
266 goldsinny wrasse life histories, and that might also have clarified a potential demograhic
267 effect of the MPAs. For instance, density-dependent growth is likely a widespread
268 phenomenon in marine fish (Lorenzen and Enberg, 2002) and is also seen for juvenile
269 Atlantic cod in our study region (Rogers *et al.*, 2011). Goldsinny wrasse typically
270 defend territories on rocky shores, and there is some evidence suggesting that territory
271 size decrease at higher population densities (Sayer, 1999). An earlier study found that
272 the abundance of wrasse is now generally higher within the Norwegian MPAs than in
273 neighbouring harvested areas (Halvorsen *et al.*, 2017a), but the temporal resolution of
274 those data do not match the growth trajectories estimated in our study. Lastly, the
275 Atlantic cod has suffered a major decline in Skagerrak, but still plays a role as an apex
276 predator on wrasses and other intermediate predators in this coastal ecosystem (Hop *et*
277 *al.*, 1992; Olsen *et al.*, 2009; Roney *et al.*, 2016). Atlantic cod tend to be larger inside
278 the MPAs but so far there is no clear sign of a recovery of population abundance
279 (Moland *et al.*, 2013a).

280 Interestingly, our study shows that, compared to fyke nets, baited traps captured
281 wrasse that typically grew to reach smaller asymptotic sizes. These are the two gear
282 types commonly used in commercial wrasse fisheries in Norway (Skiftesvik *et al.*,
283 2014). Shifting the fishery towards the use of baited traps could therefore aid in
284 protecting large-growing phenotypes (depending on gear-specific mesh sizes). As noted
285 by Berkeley *et al.* (2004a), introducing slot-size limits (i.e., a combination of minimum-

286 and maximum legal size) could also benefit fast growing fish reaching larger asymptotic
287 body sizes, in addition to a general reduction in fishing pressure. Individuals that reach
288 a larger asymptotic body size are likely to be more productive, since, for many species
289 including wrasses, there is a positive relationship between fish body length and
290 fecundity (e.g., Oosthuizen and Daan, 1974; Alonso-Fernández *et al.*, 2014). Also, there
291 is often a positive association between offspring quality and maternal size or age
292 (Trippel, 1998; Berkeley *et al.*, 2004b). Building on this, a recent study concluded that
293 current fishery models may have substantially underestimated the positive contribution
294 of larger fish to population replenishment (Barneche *et al.*, 2018).

295 We found that goldsinny wrasse growth curves differed between the sexes, with
296 males reaching a larger asymptotic size than females. Under the current management
297 regime relying on a 11 cm minimum size limit, goldsinny wrasse fisheries are therefore
298 likely to be sex-selective. In particular, many of the asymptotic body sizes of females
299 captured in baited pots fell below the 11 cm limit, while the asymptotic body sizes of
300 males captured in fyke nets were usually well above. Sex-selective fisheries could
301 impact the matings system of targeted populations via effects on sex-ratios and size-
302 structure, with potential negative consequences for population productivity (Rowe and
303 Hutchings, 2003; Zhou *et al.*, 2010; Sjørdalen *et al.*, 2018). Specifically, Darwall *et al.*
304 (1992) predicted that wrasse fisheries for the aquaculture industry could alter population
305 structure and social structures, particularly by the selective removal of larger and
306 dominant territorial males that are guarding nests. The current Norwegian wrasse
307 fisheries are known to be selective on larger nest-guarding males of corkwing wrasse
308 (Halvorsen *et al.*, 2017b). Sex-ratios nevertheless appear to be similar among coastal
309 MPAs and neighbouring fished areas, suggesting that current MPAs may need to be

310 enlarged to account for potential sexual differences in behaviour (Halvorsen *et al.*,
311 2017a).

312 In summary, our study reveals fine-scale and sex-specific life history diversity of the
313 goldsinny wrasse, which, along with several other wrasse species, is increasingly
314 harvested as cleaner fish for the aquaculture industry. Life history traits such as
315 asymptotic body size are key determinants of population productivity. Identifying and
316 maintaining life-history diversity, large-growing fish in particular, is therefore important
317 from a management perspective (Berkeley *et al.*, 2004a; Zhou *et al.*, 2010; Kuparinen *et*
318 *al.*, 2016; Barneche *et al.*, 2018). To this end, we suggest that selective fishing with
319 fyke nets should be disfavoured over fishing with baited traps, and that slot size limits
320 should be considered for additional protection of large-growing fish. Lastly, we suggest
321 that MPAs are a useful tool for long-term assessment of the impact of wrasse fisheries
322 on the demography, evolution and population dynamics of local wrasse populations (see
323 also, Alós and Arlinghaus, 2013), while current and future MPAs may need to be
324 enlarged to fully protect against size- and sex-selective fisheries.

325

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331

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543 **Figure 1:** Study area (A) in southern Norway (D), showing the four regions that were
544 sampled inside MPAs (red) and harvested control areas (green); B: Risør region, C:
545 Inner Tvedestrand fjord region, E: Outer Tvedestrand fjord region, and F: Flødevigen
546 region.

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548 **Figure 2:** The study species (A) goldsinny wrasse (photo by E. Moland, Institute of
549 Marine Research) and two examples of sampled otoliths (B). The otolith on the left is
550 from a seven year old and 159 mm long female goldsinny sampled in the outer
551 Tvedestrand region (see Figure 1). The otolith on the right is from a four year old and
552 110 mm long male sampled in the Flødevigen region. Hyaline rings (winter zones) are
553 marked with horizontal bars.

554

555 **Figure 3:** Individual goldsinny wrasse growth trajectories back-calculated from
556 distances measured on otoliths.

557

558 **Figure 4:** Goldsinny wrasse asymptotic lengths, showing the median (bold horizontal
559 line), quartiles (box) and outliers (black dots) for female (red) and male (blue) fish
560 captured in fyke nets (Fyke) and baited traps (Pot).

561

562 **Figure 5:** Goldsinny wrasse asymptotic lengths, showing the the median (bold
563 horizontal line), quartiles (box) and outliers (black dots) for fish captured in a marine
564 protected area (MPA, blue) or harvested area (Control, red) within four different regions
565 along the Norwegian Skagerrak coast: Flødevigen (Flode), Risør (Risor), inner
566 Tvedestrand fjord (TvedeInn) and outer Tvedestrand fjord (TvedeOut).

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Table 1. Summary statistics of goldsinny wrasse sampled from four MPAs and neighbouring control areas along the Norwegian Skagerrak coast in August and September 2013, showing the sample size (N) for each of the two gear types (unbaited fyke nets and baited pots) with effort (number of nets or pots) in parenthesis, mean body length and age of sampled fish (range).

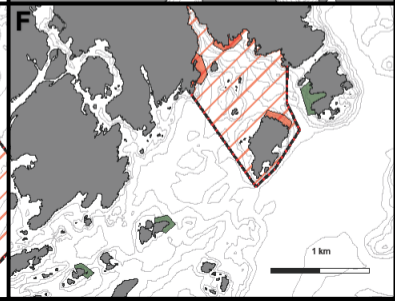
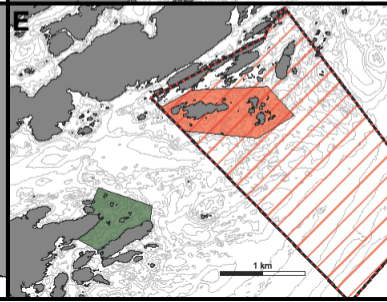
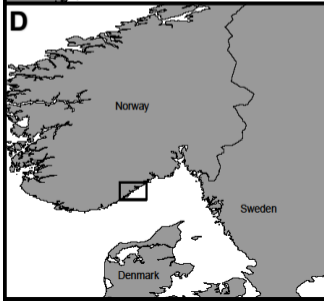
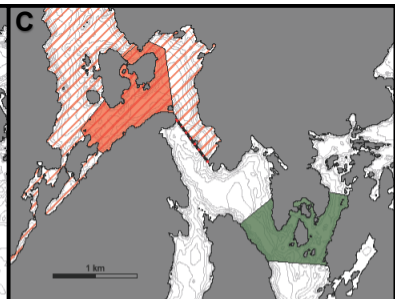
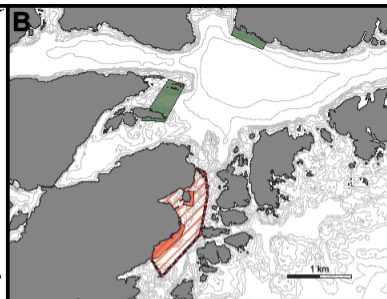
Region	Treatment	N _{fyke}	N _{pot}	Length, mm	Age, years
Flødevigen	MPA	23 (46)	118 (30)	104 (75–147)	4.1 (1–13)
	control	34 (47)	102 (31)	98 (70–129)	4.3 (2–10)
Tvedestrand inner	MPA	17 (14)	68 (8)	98 (76–133)	5.3 (2–13)
	control	50 (24)	24 (15)	106 (78–139)	4.2 (1–13)
Tvedestrand outer	MPA	48 (6)	58 (6)	107 (68–147)	3.9 (1–12)
	control	20 (9)	74 (7)	105 (81–142)	4.0 (2–8)
Risør	MPA	35 (16)	98 (12)	99 (67–128)	3.3 (1–9)
	control	29 (18)	28 (12)	107 (75–137)	3.2 (1–8)

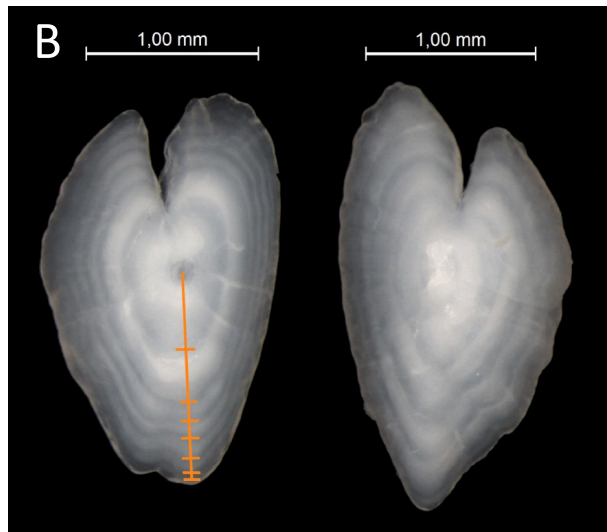
Table 2. Comparison of linear models for predicting goldsinny wrasse asymptotic body length (L_{∞}), showing the structure, R^2 value and Akaike Information Criterion (AIC) of each model. Fishing gear type (Gear) , sex, MPA treatment (Treat) and region (Reg) were included as predictor variables (factors). The most parsimonious model selected for inference is shown in bold.

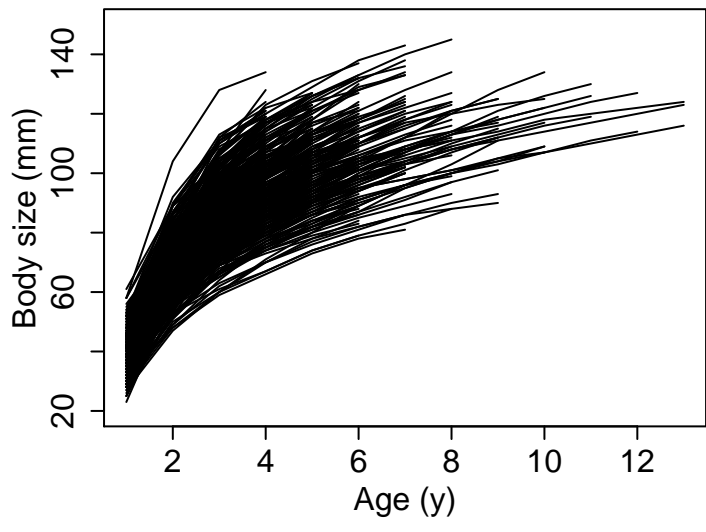
Model structure	R^2	AIC
$L_{\infty} = Sex*Gear + Sex*Reg + Treat*Reg$	0.38	-563.2
$L_{\infty} = Sex*Gear + Treat*Reg$	0.38	-564.9
$L_{\infty} = Sex + Gear + Treat*Reg$	0.37	-562.3
$L_{\infty} = Sex*Gear + Treat + Reg$	0.27	-503.8

Table 3. Parameter estimates (standard error, SE) from the most parsimonious linear model explaining variation in goldsinny wrasse asymptotic length, including effects of fishing gear type, sex, MPA treatment and region. Fyke nets, females, harvested control areas and the Flødevigen region were set as reference levels in the model.

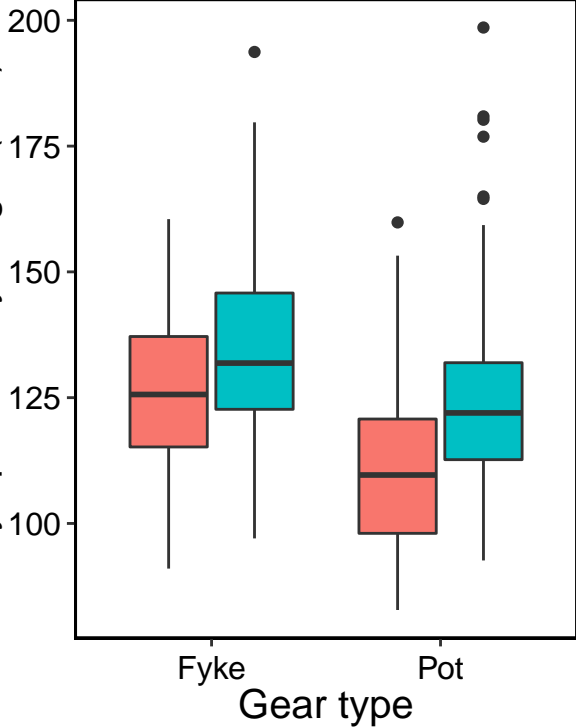
Model term	Par	SE	p-value
Intercept	4.744	0.019	<0.0001
Sex _{male}	0.071	0.019	<0.0001
Gear _{pot}	-0.096	0.018	<0.0001
Treat _{MPA}	0.093	0.019	<0.0001
Reg _{Risør}	0.125	0.033	<0.0001
Reg _{Tvedestrand inner}	0.126	0.024	<0.0001
Reg _{Tvedestrand outer}	0.100	0.022	<0.0001
Sex _{male} * Gear _{pot}	0.052	0.025	0.035
Treat _{MPA} * Reg _{Risør}	-0.127	0.041	0.002
Treat _{MPA} * Reg _{Tvedestrand inner}	-0.264	0.032	<0.0001
Treat _{MPA} * Reg _{Tvedestrand outer}	-0.063	0.032	0.046

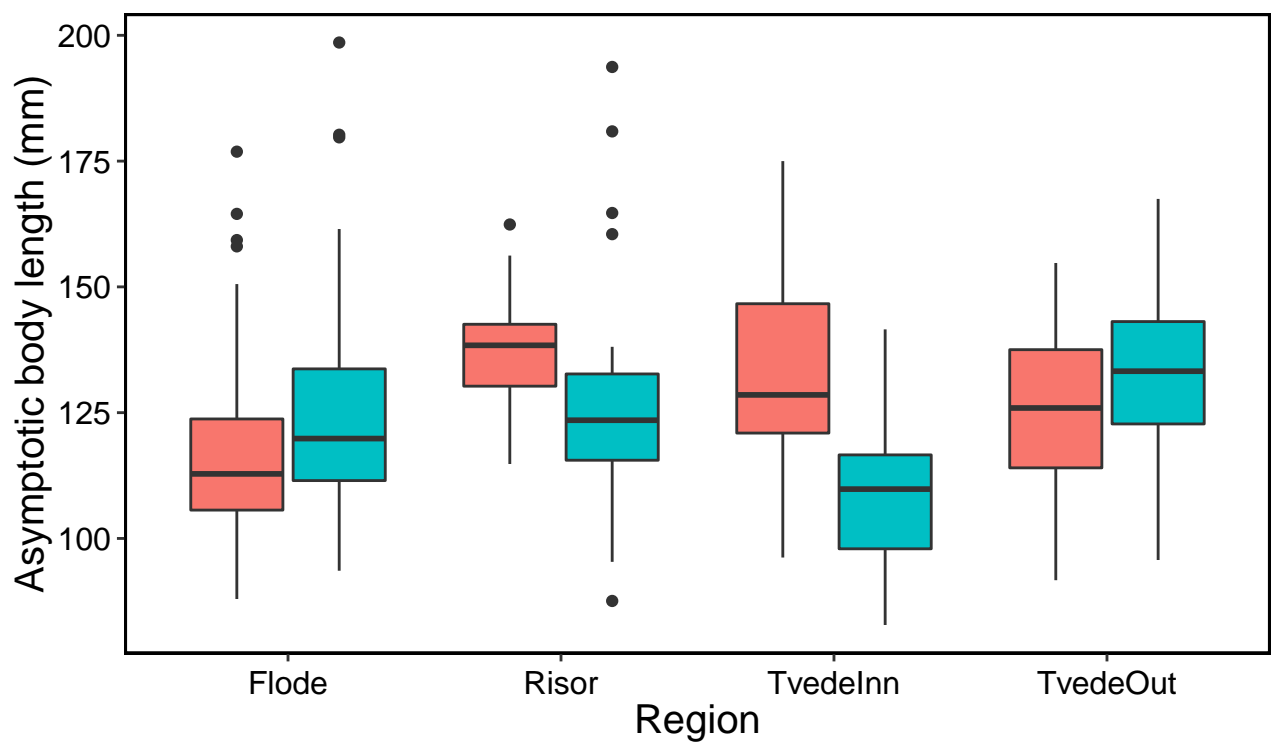




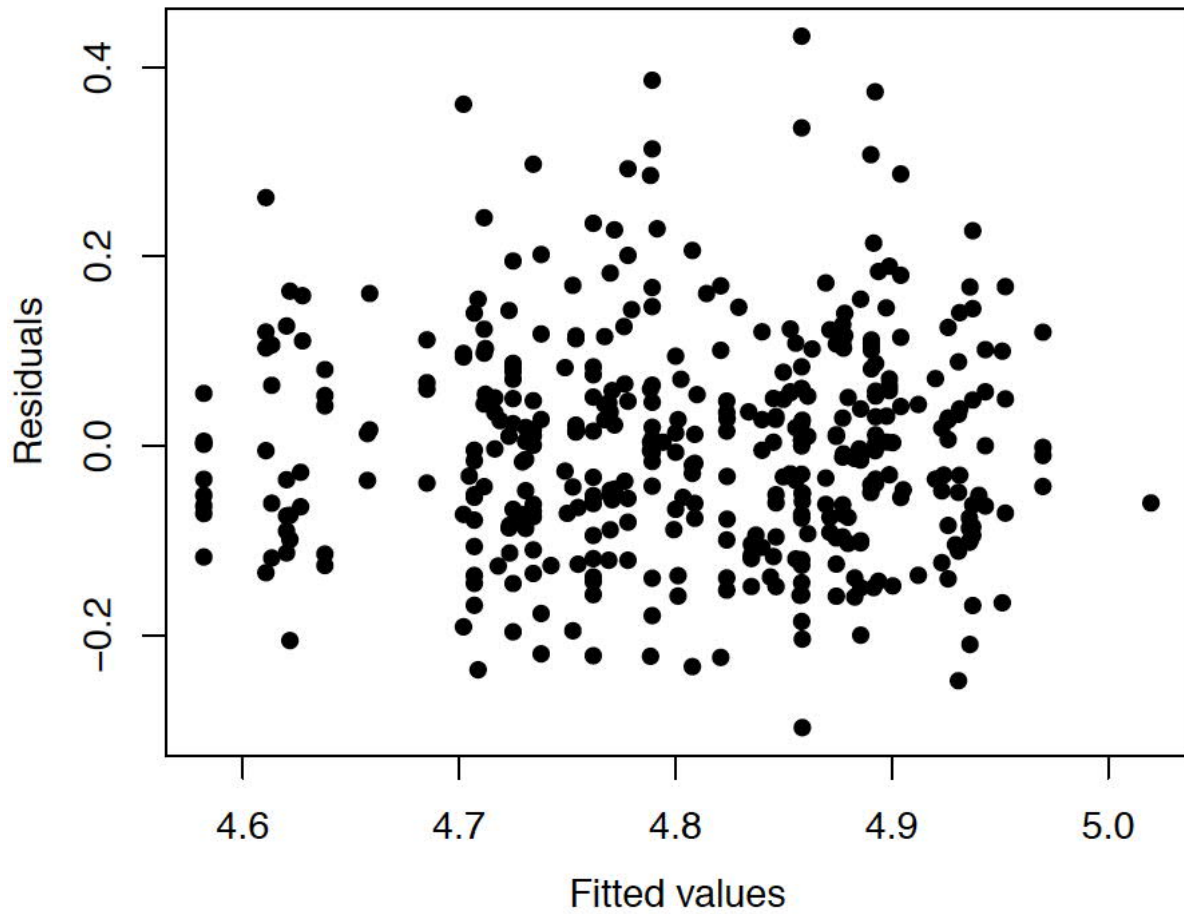


Asymptotic body length (mm)





Supplementary information



Supplementary Figure 1. Residuals versus fitted values for the most complex model used as a starting point for model selection and inference about variation in goldsinny wrasse asymptotic lengths (the response variable). For details about model structure, see Table 2.