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

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Abstract

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

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

Introduction

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

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

The goldsinny wrasse (*Ctenolabrus rupestris*) is an abundant intermediate predator distributed in shallow coastal waters of the North-East Atlantic from Morocco to Norway. The species typically prefers rocky- or vegetated substrates with access to refuges such as spaces between rocks, crevices or caves (Costello, 1991; Sayer *et al*., 1993; Gjøsæter, 2002a). Goldsinny wrasse may reach 20 years of age and a body length of 18 cm (Darwall *et al*., 1992; Sayer *et al.*, 1995). The eggs are pelagic and males defend territories up to 2 m^2 which they may keep for several years (Hilldén, 1981; Sayer, 1999). Commercial exploitation of small-bodied wrasses such as the goldsinny began in the 1990's in Norway and on the British Isles, when it was discovered that their natural behaviour as parasite cleaners on other fish (Potts, 1973) could be used to reduce sea-lice (*Lepeophtheirus salmonis* and *Caligus elongatus*) infestation in salmonid aquaculture (Darwall *et al*., 1992; Deady *et al*., 1995; Sundt and Jørstad, 1998). Already during the early wrasse fisheries there was concern about the long term sustainability of the fishery, since reductions in the abundance of larger and older fish coincided with the emergence of the fishery (Sayer *et al*., 1996; Varian *et al*., 1996). The wrasse catches remained relatively low throughout the 1990's and 2000's, when wrasses were only complementary to chemical treatments. However, more recently, the lice infestation problem in salmonid aquaculture worsened considerably and the annual landings of wild-caught wrasse in Norway have surpassed 20 million individuals (Gonzalez and de Boer, 2017). Wrasses are caught with small vessels using fyke nets and baited pots at shallow depths on rocky, kelp covered habitat (Gjøsæter, 2002b; Skiftesvik *et al*., 2015). Four different species are being harvested in Norway: the goldsinny wrasse, corkwing wrasse (*Symphodus melops*), ballan wrasse (*Labrus bergylta*) and rock cook (*Centrolabrus exoletus*). A case study from one Norwegian fjord suggests that corkwing wrasse and goldsinny wrasse hold the larger share of the landings (Skiftesvik *et al*., 2014, 2015). The official landings statistics from the Norwegian directorate of fisheries confirm this pattern, where goldsinny wrasse and corkwing wrasse each constituted ca. 45 %, followed by ballan wrasse (8 %) and rock cook (2 %) (Gonzalez and de Boer, 2017). In Norway, the first management measures for wrasse were implemented in 2011, introducing a minimum size limit of 11 cm and closure of the fishery during the spring spawning period. However, these regulations have apparently been unsuccessful in protecting mature fish, especially males (Halvorsen *et al*., 2016).

In this study, we explore fine scale spatial variation in life histories of goldsinny wrasse across a network of Norwegian coastal MPAs. Originally, these MPAs were implemented to protect and rebuild depleted populations of European lobster (*Homarus gammarus*) and are managed through gear restrictions allowing only hook and line fishing (Moland *et al*., 2013a). Therefore, the MPAs are not strict no-take marine reserves. However, wrasse fishing for the aquaculture industry is conducted with fixed gear types (fyke nets and baited traps) which are not permitted within the MPAs. Due to its small size, the goldsinny wrasse is not harvested as a food fish by anglers using hook and line (Vølstad *et al*., 2011). Wrasses are typically sedentary reef fishes with limited home ranges and may therefore benefit from small coastal MPAs (Hilldén, 1981; Villegas-Ríos *et al*., 2013). Indeed, the abundance of wrasse is now generally higher within the Norwegian MPAs than in neighbouring harvested areas (Halvorsen *et al*., 2017a). Albeit relatively small (0.6 – 5.3 km^2), the MPAs also offer partial protection to upper-trophic-level predators such as the European lobster and Atlantic cod (*Gadus morhua*), the latter being a potential predator on wrasses (Hop, 1992). On the Norwegian coast, both cod and lobster display sedentary behaviour (Moland *et al*., 2011; Villegas-Ríos *et al*., 2017) and survival rates and body size have increased within the MPAs for both species (Moland *et al*., 2013a,b; Fernández-Chacón *et al*., 2015, 2017).

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

Material and methods

Sampling and age determinations

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

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

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

where L_a is the estimated length-at-age a, L_c the length at capture, O_a the distance from the centre of the otolith to the outer edge of the annulus defining age a, and O_c the distance from the centre to the outer margin of the otolith.

Growth analyses and statistical modelling

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

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

where $L(t)$ is fish length at age t, L_∞ the asymptotic length, L_0 the average length at $t = 0$, and k the intrinsic growth rate (von Bertalanffy, 1938). Non-linear least squared regression, with L_0, L_∞ and k as free model parameters, was used to fit VB curves to the individual back-calculated growth trajectories (Pardo *et al.*, 2013). Only fish with an otolith age of four years or older were included in these analyses (n = 413), since VB curves could not be reliably fit to three data points (back-calculated lengths at age) or less. Linear models, fitted in the statistical software package R using a Gaussian error distribution (R Development Core Team, 2012), were used to investigate effects of MPAs, sex and gear type (as factors) on growth trajectories. We focussed the analyses on L_∞ as the key parameter capturing growth differences as it is strongly and negatively correlated with *k* (Charnov 1993). Region was included as a factor in the model (four levels: Flødevigen, inner Tvedestrand fjord, outer Tvedestrand fjord, and Risør). We hypothesised that potential effects of MPA treatment and sex on goldsinny wrasse growth trajectories could depend on the sampling region, and thus inclucded two-way interaction terms between these factors in the starting model (Table 2). We also hypothesised that an effect of gear type could depend on sex, perhaps due to behavioural differences, and therefore included this interaction effect in the starting model as well (Table 2). Prior to model selection data were explored following the protocol described by Zuur *et al*. (2010; see also, Zuur *et al*., 2016). One outlier with an estimated asymptotic length of 710 mm was excluded from further analyses. The response variable (L_∞) was log-transformed to improve normality. A residual plot indicated that our starting model, including all relevant factors and interaction effects, fitted the data adequately and thus provided a good starting point for model selection (Supplementary material). The Akaike information criteria AIC was used for model selection, where the model having the lowest AIC value was considered the most parsimonious one and used for inference (Burnham and Anderson, 1998). We acknowledge that some uncertainty in the response variable, associated with the fitting of VB growth curves, will not be accounted for in the linear model. However, the VB curves closely fitted the back-calculated lengths (see Results). Also, by focussing the analyses on fish that were at least four years old, our results will not be biased by incomplete juvenile growth curves with potentially greater uncertainty in parameter estimates.

Results

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

Discussion

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

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

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

Interestingly, our study shows that, compared to fyke nets, baited traps captured wrasse that typically grew to reach smaller asympotitic sizes. These are the two gear types commonly used in commercial wrasse fisheries in Norway (Skiftesvik *et al*., 2014). Shifting the fishery towards the use of baited traps could therefore aid in protecting large-growing phenotypes (depending on gear-specific mesh sizes). As noted by Berkeley *et al*. (2004a), introducing slot-size limits (i.e., a combination of minimum-and maximum legal size) could also benefit fast growing fish reaching larger asymptotic body sizes, in addition to a general reduction in fishing pressure. Individuals that reach a larger asymptotic body size are likely to be more productive, since, for many species including wrassses, there is a positive relationship between fish body length and fecundity (e.g., Oosthuizen and Daan, 1974; Alonso-Fernández *et al*., 2014). Also, there is often a positive association between offspring quality and maternal size or age (Trippel, 1998; Berkeley *et al.*, 2004b). Building on this, a recent study concluded that current fishery models may have substantially underestimated the positive contribution of larger fish to population replenishment (Barneche *et al*., 2018).

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

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

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

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

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

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

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

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).

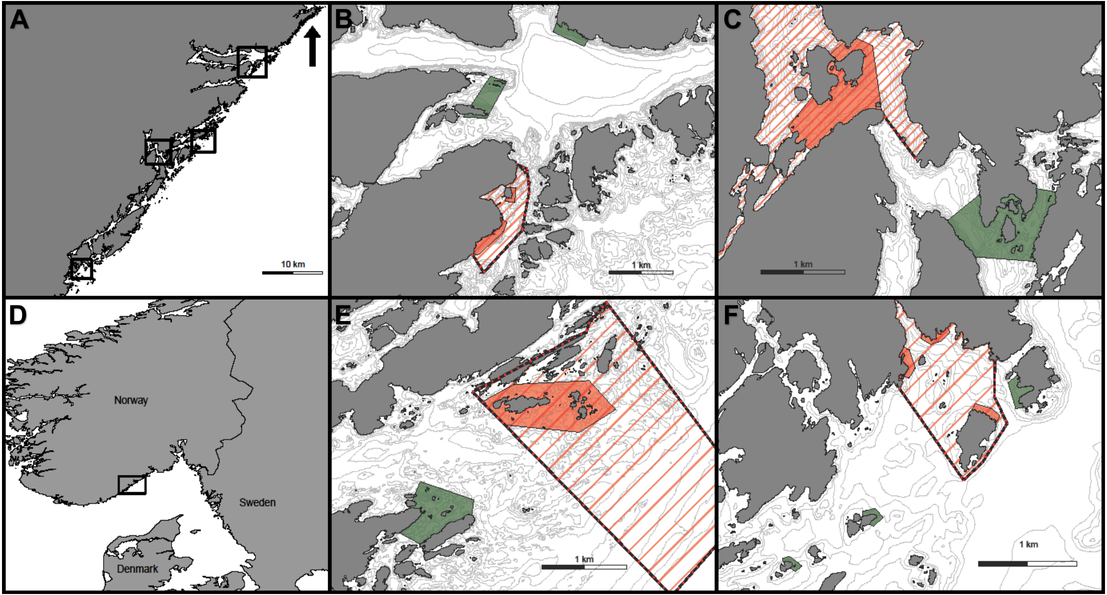
Region	Treatment	N_{fyke}	N_{pot}	Length, mm	Age, years
Flødevigen	MPA	23 (46)	118 (30)	104 (75–147)	4.1 (1–13)
	control	34 (47)	102 (31)	98 (70–129)	4.3 (2–10)
Tvedestrand inner	MPA	17 (14)	68 (8)	98 (76–133)	5.3 (2–13)
	control	50 (24)	24 (15)	106 (78–139)	4.2 (1–13)
Tvedestrand outer	MPA	48 (6)	58 (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)

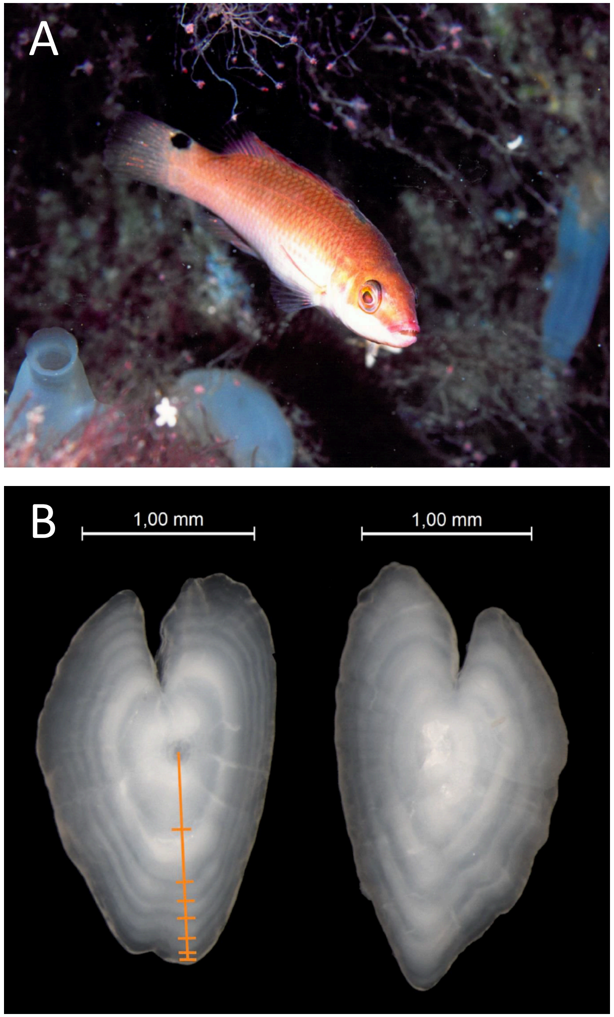
Table 2. Comparison of linear models for predicting goldsinny wrasse asymptotic body length (L_∞), showing the structure, R^2 value and Akaike Information Criterion (AIC) of each model. Fishing gear type (Gear) , sex, MPA treatment (Treat) and region (Reg) were included as predictor variables (factors).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

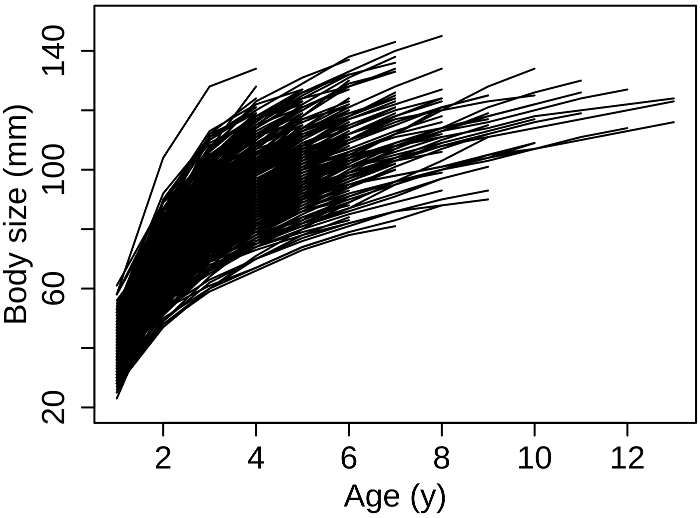
Model structure	R^2	AIC
$L_\infty = Sex*Gear + Sex*Reg + Treat*Reg$	0.38	-563.2
$L_\infty = Sex*Gear + Treat*Reg$	**0.38**	**-564.9**
$L_\infty = Sex + Gear + Treat*Reg$	0.37	-562.3
$L_\infty = Sex*Gear + Treat + Reg$	0.27	-503.8

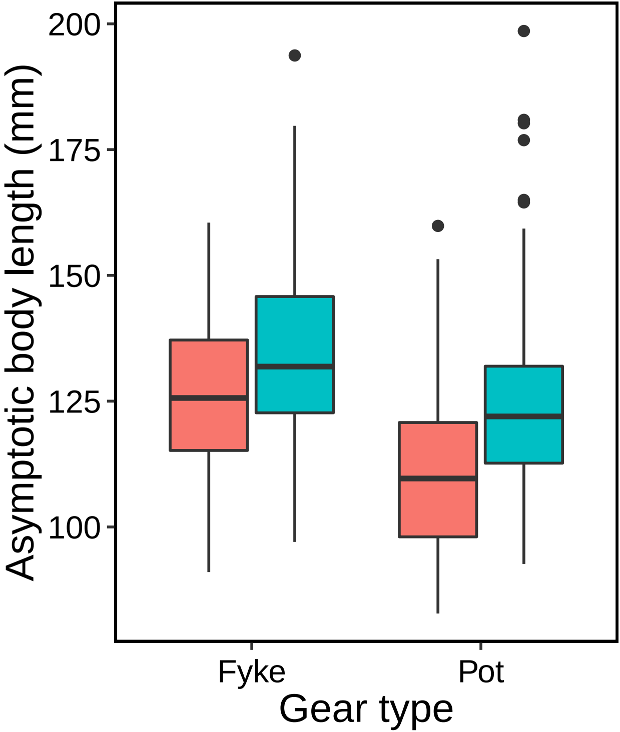
Table 3. Parameter estimates (standard error, SE) from the most parsimonious linear model explaining variation in goldsinny wrasse asymptotic length, including effects of fishing gear type, sex, MPA treatment and region. Fyke nets, females, harvested control areas and the Flødevigen region were set as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

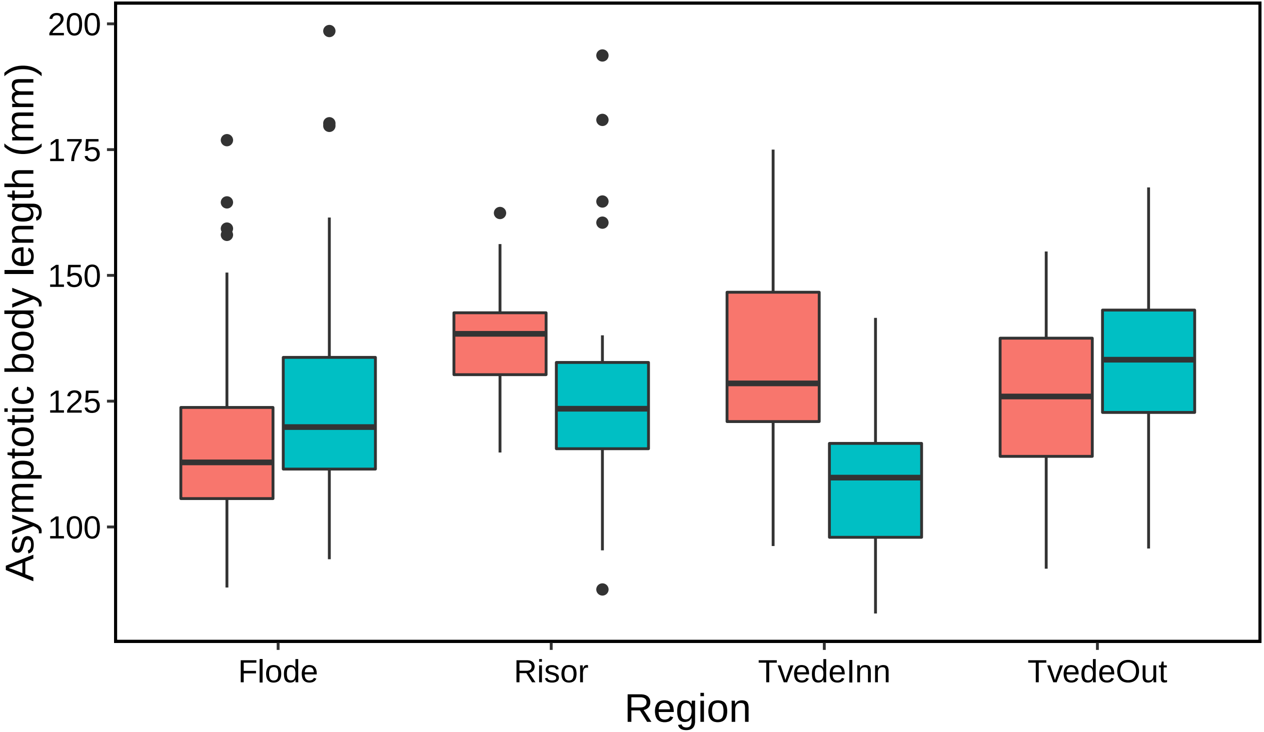
Model term	Par	SE	p-value
Intercept	4.744	0.019	<0.0001
Sex_{male}	0.071	0.019	<0.0001
Gear_{pot}	-0.096	0.018	<0.0001
$\text{Treat}_{\text{MPA}}$	0.093	0.019	<0.0001
$\text{Reg}_{\text{Risør}}$	0.125	0.033	<0.0001
$\text{Reg}_{\text{Tvedestrand inner}}$	0.126	0.024	<0.0001
$\text{Reg}_{\text{Tvedestrand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


A
10 km
B
1 km
C
1 km
D
Norway
Sweden
Denmark
E
1 km
F
1 km


A
B
1,00 mm
1,00 mm

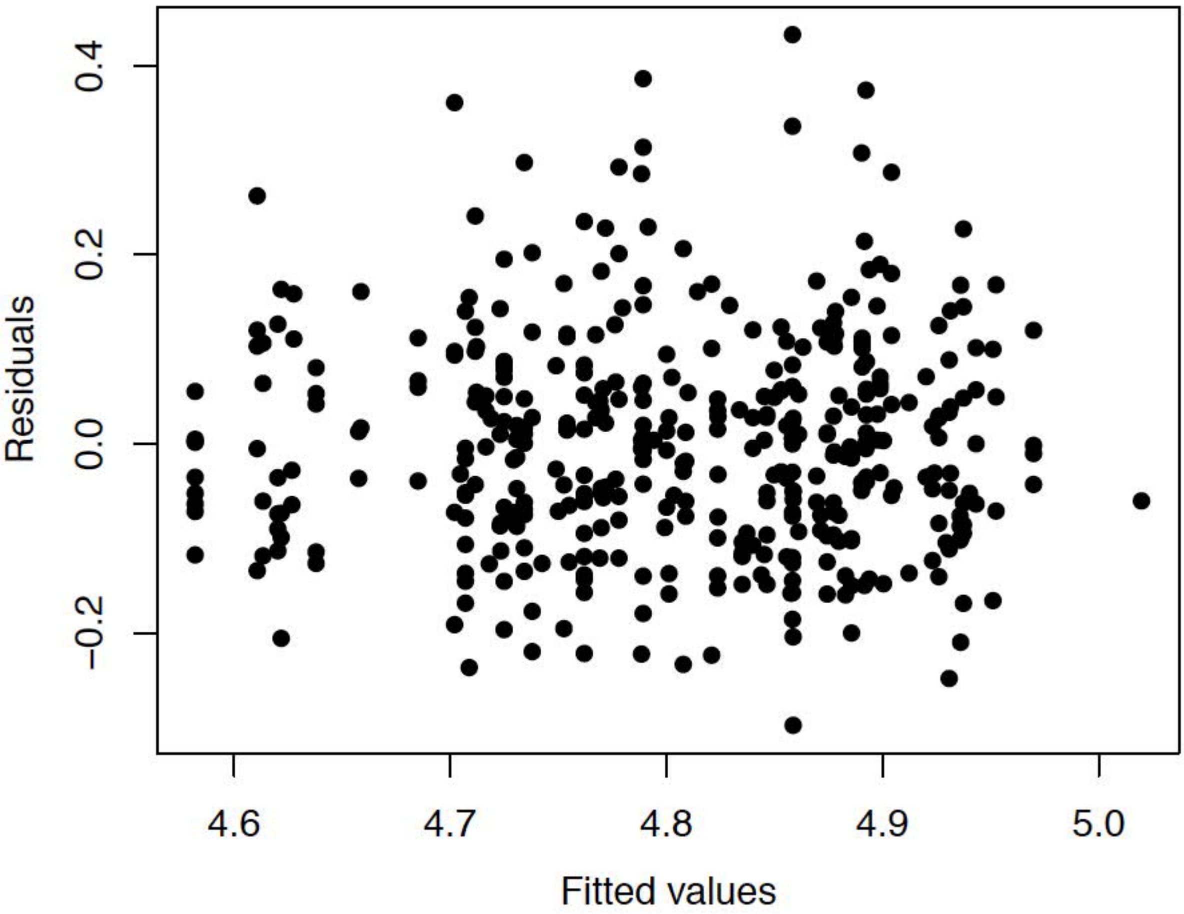

Body size (mm)
140
100
60
20
2
4
6
8
10
12
Age (y)


Asymptotic body length (mm)
200
175
150
125
100
Fyke
Pot
Gear type



Asymptotic body length (mm)
200
175
150
125
100
Flode
Risor
TvedeInn
TvedeOut
Region

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 asympototic lengths (the response variable). For details about model structure, see Table 2.