# Eurasian perch Perca fluviatilis growth and fish community structure, inside and outside a marine-protected area in the Baltic Sea

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**ORIGINAL ARTICLE**

# Eurasian perch *Perca fluviatilis* growth and fish community structure, inside and outside a marine-protected area in the Baltic Sea

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**Abstract**

Growth of Eurasian perch *Perca fluviatilis* L. and fish community structure between sites within a marine-protected area (MPA) and unprotected sites in the Baltic Sea were examined. Von Bertalanffy, logistic and Gompertz growth models were fitted to *P. fluviatilis* length at age data, and the logistic model was the most parsimonious for growth between locations. A larger mean maximum size ($L_\infty$) and a smaller instantaneous growth rate ($g$) were found within the MPA. All three models also predicted that after age seven, fish inside the MPA would be larger. Community structure differed with more *P. fluviatilis* collected outside of the MPA, and more roach *Rutilus rutilus* (L.) and bleak *Alburnus alburnus* (L.) collected inside the MPA. These growth differences may be indicative of recreational fishing effects on *P. fluviatilis* outside of the MPA, a result of complex interspecific and intraspecific species interactions, or other undetected environmental variation between locations.

**KEYWORDS**
age, Gompertz, logistic, marine protected areas, recreational fishing, von Bertalanffy

## 1 | INTRODUCTION

Marine-protected areas (MPAs) have become a popular tool for fisheries management and conservation, given that they provide refuge for overexploited fish populations and protect fish communities from fishing-induced alteration (Lester et al., 2009; Pauly et al., 2002). MPA establishment can result in increased abundance, size and biomass of fished species, as well as increased species richness within reserve boundaries (Claudet et al., 2008; Halpern & Warner, 2003; Lester et al., 2009). Networks of MPAs may be more beneficial than single sites if they include corridors for fish to migrate, preserve a wider variety of habitats, better protect localised recruitment and preserve the integrity of ecosystem-level processes (Gaines, Lester, Grorud-Colvert, Costello & Pollnac, 2010; Sundblad, Bergström & Sandström, 2011). Typically, MPAs are established in response to commercial exploitation. However, recreational fishing can produce similar effects on fish populations, including community

shifts, truncated size and age structures, early maturity and reduced maximum length (Coleman, Figueira, Ueland & Crowder, 2004; Lewin, Arlinghaus & Mehner, 2006; Westera, Lavery & Hyndes, 2003). Therefore, MPA effectiveness needs to be evaluated within this context.

In the Baltic Sea, a network approach to MPAs has been employed (Sundblad, Bergström, Sandström & Eklöv, 2014; Sundblad et al., 2011). The network was established by the Baltic Marine Environment Protection Commission–Helsinki Commission (HELCOM) and the Natura 2000 (Borg, Kaaria & Zweifel, 2016). The HELCOM MPAs consist of 174 sites covering 53,642 km$^2$ and many overlap with marine habitats of Natura 2000 sites (Borg et al., 2016). The Natura 2000 sites comprise 6% of all European Union marine territory, and these areas include the MPAs within the Åland Islands of Finland (European Commission, 2017).

Recreational fishing is popular in the Nordic countries and Baltic Sea (Toivonen et al., 2004). Eurasian perch *Perca fluviatilis* L.,

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pikeperch *Sander lucioperca* (L.) and pike *Esox lucius* L. are prevalent fishery species (Anon, 2005) experiencing population declines that have been attributed to overexploitation, habitat loss, anthropogenic eutrophication and recruitment failure (Adjers et al., 2006; Bonsdorff, Blomqvist, Mattila & Norkko, 1997; Mustamäki, Bergström, Ådjers, Sevastik & Mattila, 2014). In Finland, recreational fishing remains a popular and economically valuable activity. During 2004, there were 1.9 million recreational anglers in 1 million households and the total landings amounted to 38 million kg, worth EUR 46 million. *Perca fluviatilis* and *E. lucius* comprised 50% of the total catch, and *S. lucioperca* was another prevalent species (Anon, 2005).

The Åland Islands are a small semi-autonomous region of Finland located in the Baltic Sea between Sweden and Finland where recreational fishing is one of the main tourism industries and pastimes (Salmi, Toivonen & Mikkola, 2006). In 2014, it was estimated that recreational fishers harvested 662,000 kg of *P. fluviatilis* in the Åland Islands (Moilanen, 2015). In these Islands, 11,000 fishermen, representing 41% of the population and 46% of all households, participate in recreational fishing using a variety of gear types, including hook and line, spinning rod, gillnet, jig, fly rod and trolling gear (Anon, 2005).

*Perca fluviatilis* is a particularly popular recreational fish species in the Baltic Sea and Åland Islands and has shown declines throughout most of the Baltic (Adjers et al., 2006; Nilsson, Andersson, Karas & Sandstrom, 2004). *Perca fluviatilis* is widely distributed in both fresh and brackish waters (Lappalainen, Rask, Koponen & Vesala, 2001; Snickars et al., 2010) and spawning occurs in late April through June. This fish can approach a maximum length of approximately 400 mm and differing growth rates have been found along latitudinal gradients (Heibo, Magnhagen & Vøllestad, 2005) and between males and females (Mooij, Van Rooij & Wijnhoven, 1999). Most ageing studies for *P. fluviatilis* have used opercular bones (Machiels & Wijsman, 1996; Mooij et al., 1999), but given the similarity between *P. fluviatilis* and yellow perch *Perca flavescens* L. (Thorpe, 1977), otoliths are likely a superior ageing structure, especially for older fish (Niewinski & Ferreri, 1999; Vandergoot, Bur & Powell, 2008).

Considering the population declines of recreational species and the prevalence of recreational fishing throughout the Nordic Countries, it is imperative to determine the ecological and biological effectiveness of MPAs within exploited recreational fishing areas. Therefore, the first objective of this study was to compare growth and condition of *P. fluviatilis* between two locations inside and outside of an MPA, within the Natura 2000 network in the Åland Islands of Finland, to determine the effects of recreational exploitation. The second objective was to compare the community structure of fishes between these locations, to evaluate how fishing pressure and protection from fishing pressure may affect the fish community. This study should ultimately provide insight into MPA functionality in popular recreational fishing areas of the Baltic Sea, and this knowledge can prove useful in recovery programmes for exploited recreational fisheries elsewhere.

## 2 | MATERIALS AND METHODS

### 2.1 | Field sampling

The MPA sampling location was adjacent to the Husö biological station. This station is located within the Åland Islands of Finland and the waters surrounding the station have been functionally closed to fishing and habitat modification, due to scientific use, since the station was established in 1959. The MPA is 0.727 km$^2$ and was formally established when the Natura 2000 network was implemented in EU countries, because the waters surrounding Husö are sheltered and have high densities of submerged aquatic vegetation (SAV) protecting critical nursery and spawning habitat of fishes (Snickars et al., 2005, 2009, 2010). This MPA was also established because of increasing fishing pressure on perch and pike, given the popularity of sport fishing in the Åland Islands (Anon, 2005, Moilanen, 2015; Salmi et al., 2006). The location sampled outside of the MPA was approximately 3.1 km north of the MPA boundary, and sampling sites were chosen haphazardly in both locations based on pre-determined depth and habitat parameters (Figure 1). Specifically, shorelines of both inside and outside sites consisted of *Phragmites australis* reed beds, water depths were at least 2 m, and SAV was present in all sites.

Fish were collected with Nordic coastal gillnets at eight sampling events between 22 and 31 August 2016. The nets were 45-m long, 1.8-m high, and consisted of nine different panels with varying mesh sizes (30, 15, 38, 10, 48, 12, 24, 60 and 19 mm). Nets were deployed between 19:00 and 21:00 (before sunset) and hauled between 07:00 and 09:00 (after sunrise). During each sampling event, two gillnets were set at one site in each location. One net was set perpendicular to the *P. australis* reeds (deployed from the water edge of the reed bed) and one parallel (50 m off the reed bed edge). Each net was fished on the bottom and the two nets were spaced 50 m apart. Sampling sites, within each location, were spaced at least 100 m apart. During each net haul, abiotic parameters (temperature, salinity and pH) were measured using a handheld YSI meter. To determine turbidity, water samples were taken using acid washed LDPE bottles and measured on a turbidimeter, and SAV was sampled using a benthic rake. The presence of anglers or fishing gear was also recorded during each sampling event.

### 2.2 | Sample processing and otolith ageing

During gillnet hauls, *E. lucius* were counted and released live in the field at the collection site, due to conservation concerns. After net hauls, fish in gillnets were returned to the laboratory as quickly as possible and placed on ice. This anesthetised all fishes through hypothermia, and euthanised small fishes (<5 cm) (Jenkins et al., 2014). For *P. fluviatilis* that remained alive after being placed on ice, the spinal cord was carefully and quickly severed below the otic capsule to euthanise these fish as quickly as possible, while keeping the otoliths intact. Other large fishes (e.g. *T. tinca* (L.), *Carassius carassius* (L.))
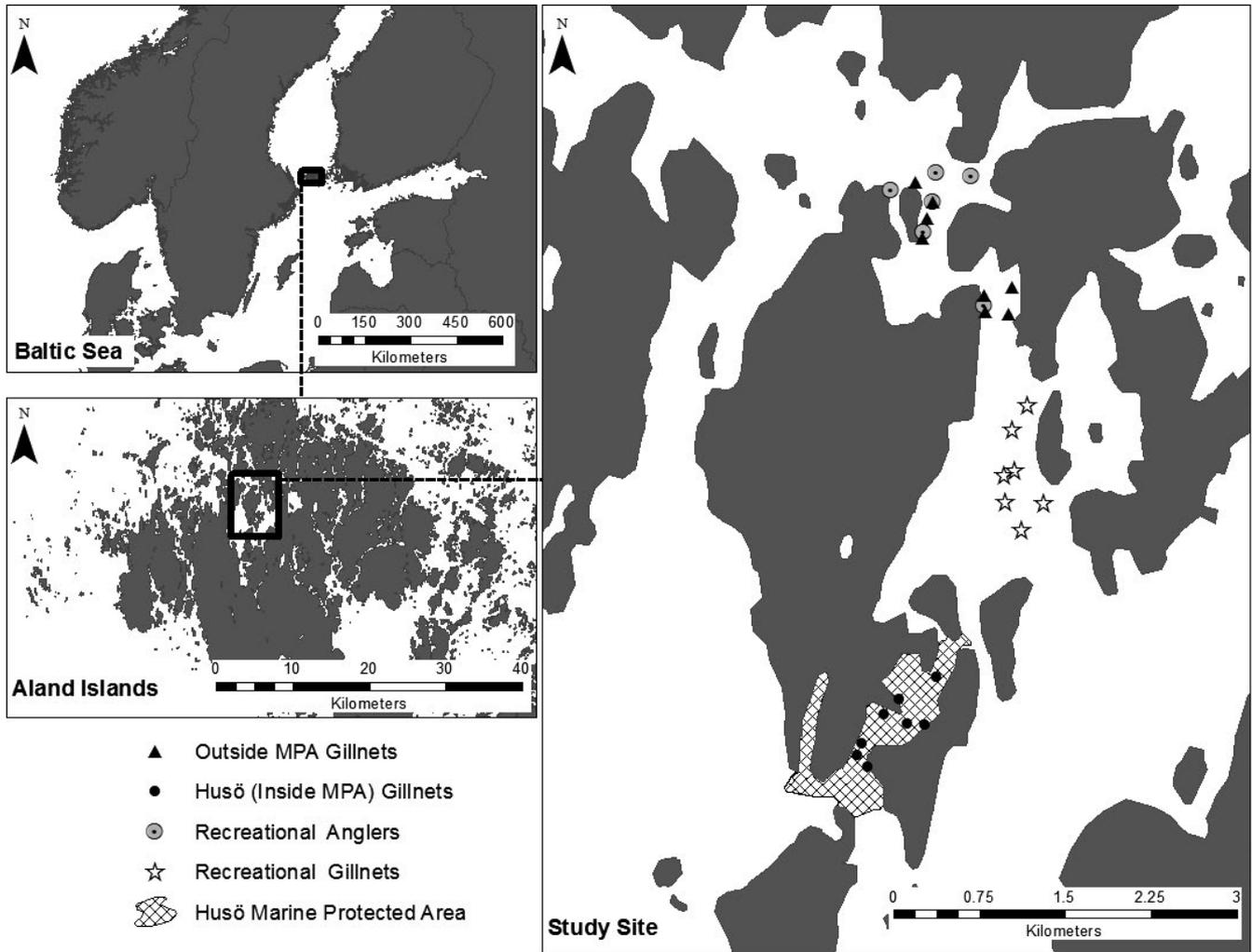
**FIGURE 1** Sampling locations in the Åland Islands, Finland. The eight Husö gillnet sites inside of the marine-protected area (MPA) are designated as black circles. The eight outside MPA gillnet sites are designated with triangles. Locations of observed recreational gillnets are denoted with stars and observed angler effort is grey circles with a dot in the middle. The cross-hatched polygon represents the Husö MPA

that remained alive were quickly removed from gillnets, measured, weighed and released back into the water at the MPA location. After the remaining fish were removed from the gillnets, all fish except for *P. fluviatilis* were counted and mass weighed by species. Each *P. fluviatilis* was measured (total length [TL, mm]), weighed (total and gonad weight, g), sexed, and the sagittal otoliths were removed.

Otolith ageing was carried out at the Dauphin Island Sea Lab (DISL), Alabama, USA. The right otolith was preferentially used (left otolith used if right not present) and was embedded in epoxy, sectioned using a Buehler low speed saw, and mounted to a slide for ageing. Each section was aged (*n* = 685) under a microscope and opaque annuli were counted by starting at the otolith core and working outward to the otolith edge (Vandergoot et al., 2008). Otolith edges were assigned a margin code of 1–4 and the final age was adjusted accordingly. Specifically, if a 3 or a 4 code was assigned, then 1 year was added to the final age (VanderKooy, 2009). This type of analysis was necessary because annulus formation was likely to occur during the sampling period; also, annulus timing is not consistent among all age classes (Blackwell & Kaufman, 2012). Otoliths

were aged by two independent readers and the average percent error (Beamish & Fournier, 1981) was 5.02%. In the event of a disagreement between Reader 1 and Reader 2, a third reader (Reader 3) aged the otolith. The final age assigned to the fish was the agreed age between Readers 1 and 3 or between Readers 2 and 3.

## 2.3 | Statistical analyses

Differences in salinity, temperature, pH, turbidity and net depths between locations were assessed using a Welch two-sided *t* test for each variable using R (R version 3.2.5 [2016-04-14]). For each net type (perpendicular and parallel), a depth measurement was taken at both endpoints, and the mean of these two points was used as the net depth. The depth between locations for perpendicular and parallel nets was tested separately for each net type. Assumptions of normality were checked using the Shapiro test. If normality assumptions were not met, a Wilcoxon rank sum test was performed.

Multivariate community analyses were performed in PRIMER 6. An analysis of similarity (ANOSIM) tested both species

abundance and biomass data to determine whether fish communities significantly differed inside and outside of the MPA. Data were standardised and square root transformed, and a Bray–Curtis similarity resemblance matrix was produced prior to this analysis. A similarity percentages (SIMPER) was run following the ANOSIM to determine which species were contributing to the difference in communities for both abundance and biomass. Abundance catch-per-unit-effort (CPUE) was defined as the total number of fish per species collected at each location during each sampling event. Biomass CPUE was calculated as the total mass of each species (g), collected at each location during each sampling event. For species that contributed to 75% of the abundance or biomass difference, Welch two-sided $t$ tests were performed for abundance and biomass CPUE to determine whether locations had significantly different species-specific abundance or biomass. Assumptions of normality were checked using the Shapiro test, and if normality assumptions were not met, Wilcoxon rank sum tests were used.

All subsequent analyses were performed in R. To compare *P. fluviatilis* condition between locations, relative condition (Le Cren, 1951) and gonadosomatic index (GSI) were compared for all fish, males only and females only using a Welch two-sided $t$ test. A Wilcoxon rank sum test was used if normality assumptions were not met. For GSI analyses ($n = 603$), all fish with unknown sex or fish with gonad weight too small to register (<0.1 g) were omitted from analyses. For sex-specific condition analyses ($n = 673$), all fish of unknown sex were removed.

Mean length, weight and age were compared among locations and sexes using a two-way ANOVA that included location, sex and the interaction between these two variables. A Tukey-HSD post hoc test was performed on each ANOVA to determine differences among groups. Assumptions of equal variance and normality were evaluated using the Levene and Shapiro tests, respectively. For these analyses, all fish with unknown sex were omitted ($n = 673$ fish remained in analyses). A Kolmogorov–Smirnov test (K–S test) was used to determine whether age and length distributions were significantly different inside and outside of the MPA (Ogle, 2016), and age and length frequency (50 mm bins) histograms were produced for visual comparison.

To describe fish growth, and compare among sexes or locations, two separate sets of three-parameter von Bertalanffy (vB), logistic (Log), and Gompertz (Gptz) growth models (Ricker, 1975, 1979) were fitted to the *P. fluviatilis* length at age data ($n = 685$), using nonlinear least squares regression (nls function) in R. For comparisons between sexes ($n = 661$), fish of unknown sex were removed before analysis. Each set of candidate models ranged from the simplest common model, with one value for each parameter, to the most complex general model that included two values (one for each sex or location) for each parameter (Ritz & Streibig, 2008). This resulted in eight candidate models for each model type to describe fish growth in terms of either sex or location.

The general three-parameter von Bertalanffy growth model is the following equation,

$$L_t = \begin{cases} L_\infty[a] * \left(1 - e^{(-K[a]*(t-t_0[a]))}\right) \\ L_\infty[b] * \left(1 - e^{(-K[b]*(t-t_0[b]))}\right) \end{cases}$$

where $L_t$ is the estimated length at age ($t$), $L_\infty$ is the asymptotic maximum length reached by individuals in the study population, $K$ is a growth coefficient that describes how quickly the maximum length is attained and $t_0$ is an extrapolation of data to fix the position of the curve along the $x$-axis (Quist, Pegg & DeVries, 2012). The $a$ and $b$ terms represent either male, female or inside, outside the MPA depending on whether sex-specific or location-specific growth is being investigated. The general three-parameter logistic growth model is the following equation,

$$L_t = \begin{cases} \dfrac{L_\infty[a]}{1+c[a]e^{-g[a]t}} \\ \dfrac{L_\infty[b]}{1+c[b]e^{-g[b]t}} \end{cases}$$

where, $L_t$, $L_\infty$, $t$, $a$, and $b$ are the same as the vB models. The remaining parameters are the inflection point of the curve ($c$) and the instantaneous growth rate ($g$) when $L_t$ approaches zero. The general three-parameter Gompertz growth model is:

$$L_t = \begin{cases} L_\infty[a] * e^{-e^{-g[a](t-t_0[a])}} \\ L_\infty[b] * e^{-e^{-g[b](t-t_0[b])}} \end{cases}$$

where $L_t$, $L_\infty$, $t$, $a$, and $b$ are the same as the vB and Log models. The remaining parameters are the instantaneous rate of growth ($g$) when $t$ equals the age that growth starts to decrease ($t_0$), and the inflection point of the curve is when $t$ equals $t_0$.

To ascertain the most parsimonious model within each type (vB, Log, Gptz), and determine whether parameters were significantly different for each sex or location, candidate models of the same type were compared by pairs in a hierarchical framework. Complex models were tested against simpler models with fewer parameters using an $F$-test on the residual sum of squares (RSS), and a non-significant result demonstrated that the two models in question fit the data equally well (Motulsky & Ransnas, 1987). This process was concluded when a simpler model did not fit the data as well as a more complex one (Motulsky & Ransnas, 1987; Ogle, 2013). If multiple models with the same number of parameters fit the data as well as a more complex model, the model with the lowest RSS was selected as the most parsimonious. If the best-fitting model had two values for any parameter, those multivalue parameters were significantly different for either sex or location. Assumptions of homoscedasticity and normality were checked for the most parsimonious models through visual inspection of the residual frequency and the residual vs fitted plot. Ninety-five percent confidence intervals (95% CI) of parameter estimates generated from the most parsimonious model of each type, for sex and location were obtained using a bootstrapping procedure (nlsBoot in R) with 10,000 iterations, given that this is the most robust way to produce these estimates for nonlinear regression (Motulsky & Ransnas, 1987; Ogle, 2013). The most parsimonious model among

types was the one with the lowest Akaike Information Criteria (AIC), given that the hierarchical approach only works for nested models of the same structure.

## 3 | RESULTS

### 3.1 | Age composition and growth

Of the 699 *P. fluviatilis* collected, 685 were used for age analyses as some otoliths were damaged or deemed unreadable. A total of 210 fish from inside the MPA and 475 fish from outside the MPA, consisting of 250 males and 411 females, were used for analyses. Also, more females (inside = 110, outside = 301) were collected than males (inside = 94, outside = 156) at both locations, and females were older than males ($F_{1,657} = 26.19$, $p < .001$, Figure 2a). Overall, more fish from each age class were collected from outside than inside the MPA. Mean age did not differ between locations ($F_{1,657} = 1.73$, $p = .189$, Figure 2a), but the age frequency distributions were significantly different (D = 0.166, $p = .001$, Figure 3a, 3b). As fish age

increased, the numbers of fish from each age class collected from each location converged; the oldest fish (age 13) was collected inside the MPA (Figure 3a).

The most parsimonious von Bertalanffy, logistic and Gompertz growth equations for sex generated a shared $L_\infty$ value (Table 1, Figure 4), demonstrating that there was no significant difference in mean maximum length between sexes. Of the three model types, the Gompertz growth equation was the best-fitting model, and it produced equal $L_\infty$ (300 mm) and $t_0$ (1.54) parameters between sexes. Males and females had significantly different instantaneous growth parameters $g$ (0.24, 0.40, respectively), indicating that females exhibited a faster growth rate than males. Model assumptions were met based on visual inspection of the residual plots.

In models comparing fish growth inside and outside of the MPA, both sexes were pooled because the $L_\infty$ parameter did not differ by sex for any of the model types, and the only unequal parameter in the most parsimonious model was the instantaneous growth parameter ($g$). The best-fitting model for fish growth inside and outside the MPA was the logistic growth model with differing parameters for
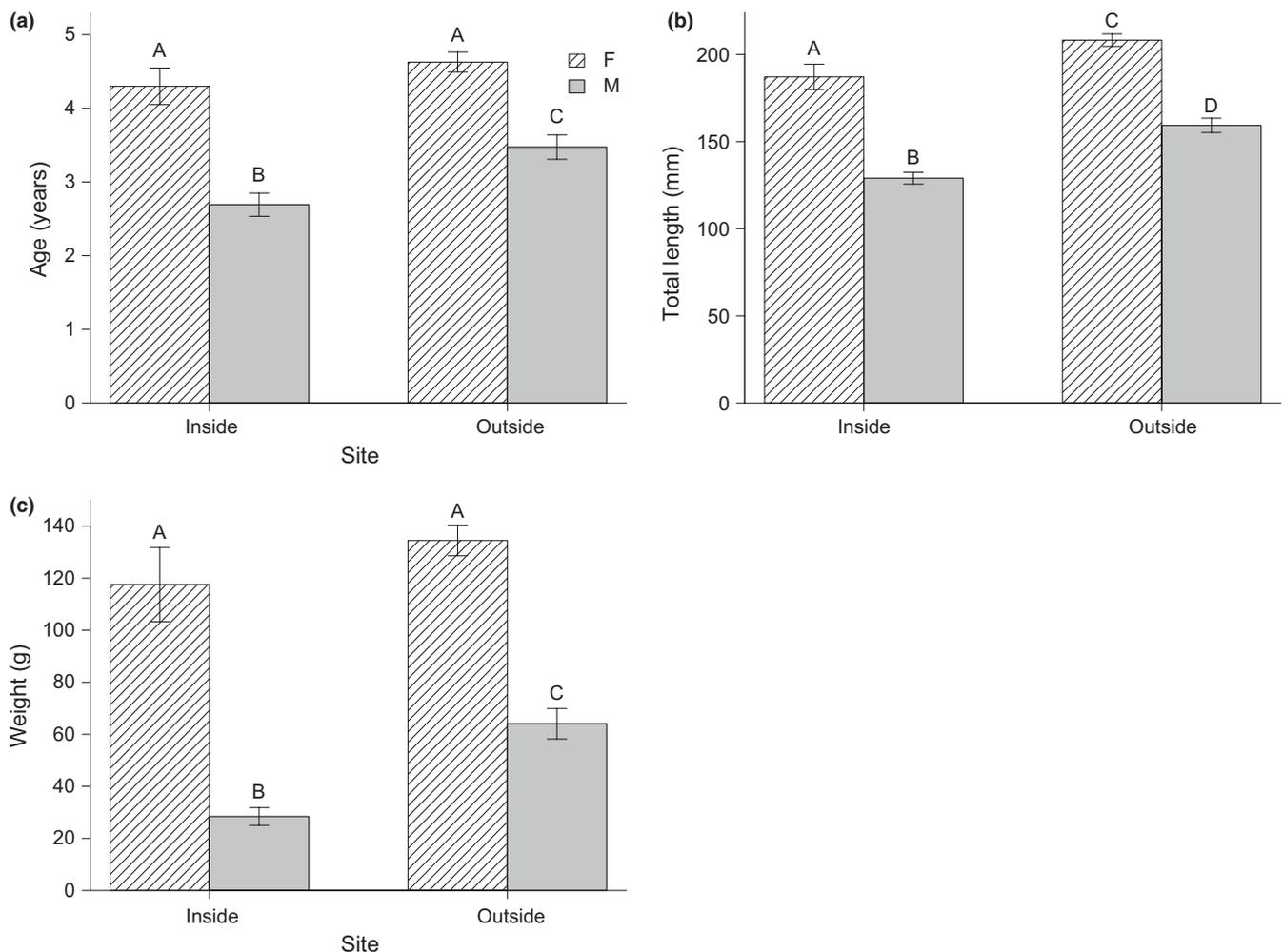


**FIGURE 2** Mean age ± 1 *SE* (a), total length ± 1 *SE* (b), and weight ± 1 *SE* (c) of female and male fish, inside and outside of the marine-protected area (MPA). Different letters above bars represent significantly different groups
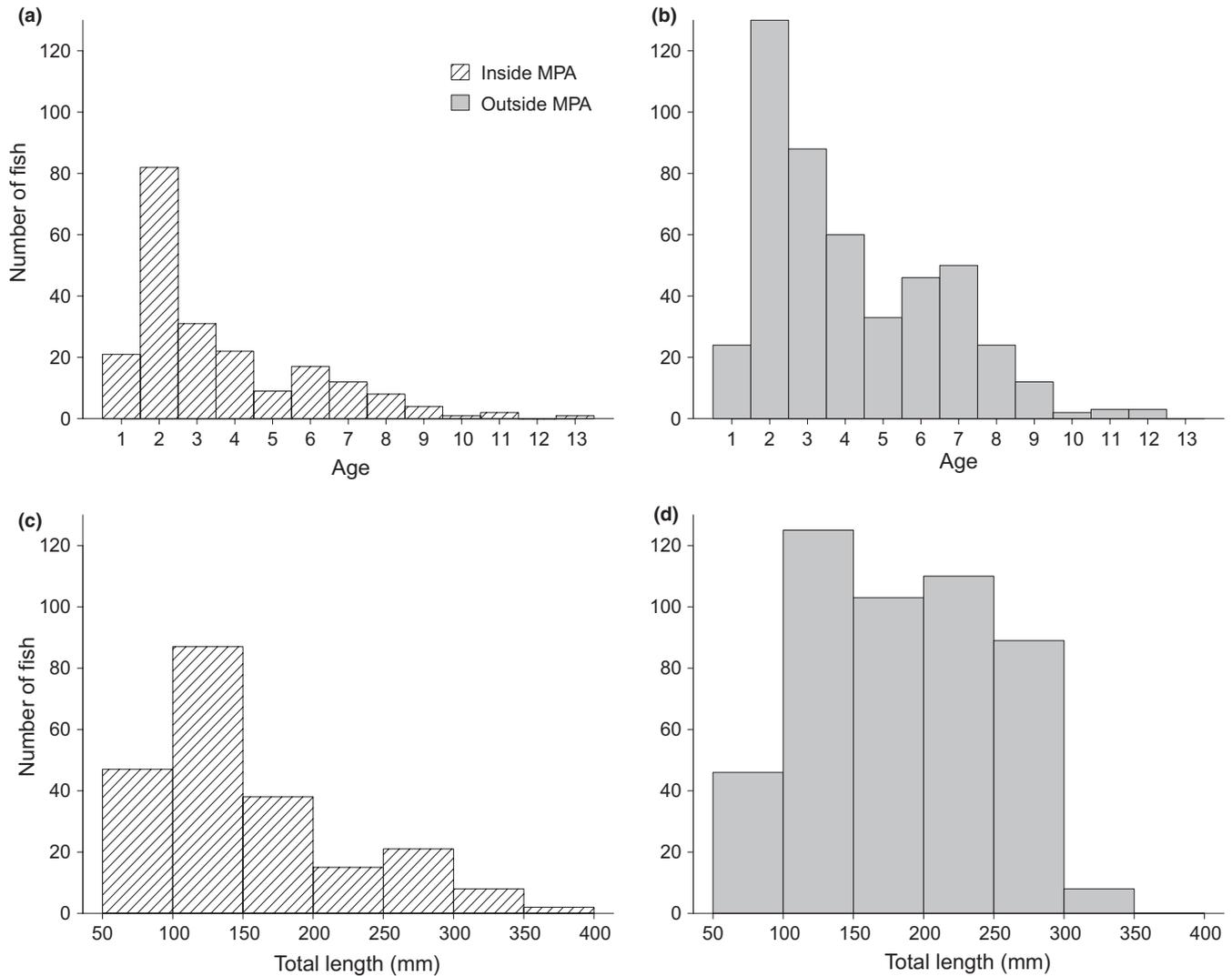
**FIGURE 3** Age frequency distributions, number of fish in each age class collected inside (a) and outside (b) of the marine-protected area (MPA) and length frequency distributions, number of fish collected in 50 mm length bins inside (c) and outside (d) of the MPA. Plots from inside the MPA (a, c) have bars that are cross-hatched

$L_\infty$ (358 and 274 mm, respectively) and $g$ (0.33, 0.61, respectively), and an equal inflection point ($c$) between locations at an age of 3.92 (Table 2, Figure 5). Therefore, *P. fluviatilis* inside the MPA were predicted to grow larger, but reach their maximum size at a slower rate, whereas fish outside of the MPA exhibited faster growth early in life, but were predicted to reach smaller sizes on average. The best-fitting models within each model type (vB, Log, Gptz) also had very similar curves (Figure 5). All three curves predicted that *P. fluviatilis* inside the MPA would be smaller than outside fish from ages two through seven, and larger after age seven (Figure 5). Model assumptions were met based on visual inspection of the residual plots.

## 3.2 | Condition, length and weight

Relative condition was not significantly different between locations when all *P. fluviatilis* ($W = 51,842$, $p = .81$), males ($W = 8,464$, $p = .23$) or females ($W = 15,388$, $p = .12$) were compared. Similarly,

GSI did not differ significantly between locations for all *P. fluviatilis* ($W = 37,553$, $p = .46$), males ($W = 6808.5$, $p = .78$), or females ($W = 10,926$, $p = .08$). Mean *P. fluviatilis* length was greater outside the MPA ($F_{1,669} = 10.35$, $p = .001$, Figure 2b) and females were longer than males ($F_{1,669} = 50.54$, $p < .001$, Figure 2b). Fish weight did not differ between locations ($F_{1,669} = 2.36$, $p = .125$, Figure 2c), but females were heavier than males ($F_{1,669} = 41.77$, $p < .001$, Figure 2c). ANOVAs for length and weight failed both normality and variance assumptions. However, these tests were still deemed appropriate, given that ANOVAs are robust to assumption violations (Brownie & Boos, 1994; Kahn & Rayner, 2003; Underwood, 1997). Although mean fish length was greater outside, the three longest and heaviest fish were collected inside the MPA (396 mm resp. 968.1 g, 357 mm resp. 588.3 g, 347 mm resp. 482.5 g) and the length frequency distributions between locations were significantly different ($D = 0.277$, $p < .001$, Figure 3c, 3d).

| Growth between sexes | | | | |
|---|---|---|---|---|
| **Parameter** | **Estimate (95% CI)** | **AIC** | **Δ AIC** | **AIC weight** |
| von Bertalanffy | | | | |
| $L_\infty$ – F/M | 325.32 (307.76 to 349.40) | 6300.15 | 4.50 | 0.09 |
| $K$ – F | 0.24 (0.19 to 0.28) | | | |
| $K$ – M | 0.14 (0.12 to 0.17) | | | |
| $t_0$ – F | −0.19 (−0.49 to 0.06) | | | |
| $t_0$ – M | −1.38 (−1.90 to −0.95) | | | |
| Logistic | | | | |
| $L_\infty$ – F/M | 288.18 (279.81 to 298.23) | 6303.44 | 7.79 | 0.02 |
| $c$ – F | 3.76 (3.29 to 4.35) | | | |
| $c$ – M | 2.62 (2.33 to 2.95) | | | |
| $g$ – F | 0.56 (0.50 to 0.63) | | | |
| $g$ – M | 0.34 (0.30 to 0.38) | | | |
| Gompertz | | | | |
| $L_\infty$ – F/M | 300.36 (290.28 to 312.48) | 6295.65 | 0.00 | 0.89 |
| $g$ – F | 0.40 (0.35 to 0.44) | | | |
| $g$ – M | 0.24 (0.21 to 0.27) | | | |
| $t_0$ – F/M | 1.54 (1.42 to 1.68) | | | |

**TABLE 1** Parameter estimates and 95% confidence intervals (95% CI) obtained from bootstrapping (10,000 iterations), Akaike information criterion (AIC), Δ AIC, and AIC weight for the most parsimonious von Bertalanffy, logistic, and Gompertz growth models used to describe *P. fluviatilis* growth between females (F) and males (M)
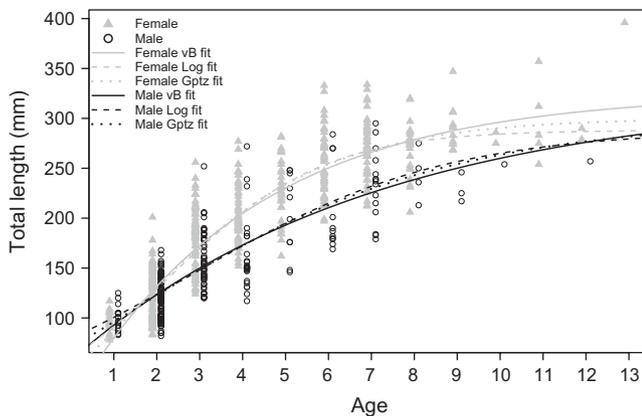


**FIGURE 4** Total length (TL) at age for female (*n* = 422) and male (*n* = 251) *P. fluviatilis*. The growth curve for each sex is shown that was obtained from the most parsimonious von Bertalanffy (vB), logistic (Log), and Gompertz (GPTZ) growth equations. The Gopertz curve was the best-fitting model among all types and both sexes had all parameters in common, except for the instantaneous growth rate (*g*)

## 3.3 | Fish community structure

Twelve fish species or species groups were collected in gillnets throughout the course of the study. All specimens of bream (*Blicca bjoerkna* (L.), *Abramis brama* (L.) and hybrids between the two species) were combined and considered as one species group due to similarities in identifying characteristics and ecosystem functions among these species. Eleven species were collected inside the MPA and nine were collected outside the MPA (Table 3). ANOSIM analyses

showed that the fish community structure was significantly different between the two locations when either abundance (R = .831, *p* = .002) or biomass (R = .747, *p* = .001) metrics were used. SIMPER analyses revealed that bleak *Alburnus alburnus* (L.), *P. fluviatilis*, roach *Rutilus rutilus* (L.), bream, and rudd *Scardinius erythrophthalmus* (L.) were responsible for 75% of the dissimilarity between locations for abundance and *R. rutilus*, *P. fluviatilis*, *A. alburnus*, *C. carassius* and *S. erythrophthalmus* were responsible for 75% of the dissimilarity for biomass.

The abundance CPUE (number of fish/162 m² gillnet/location/sampling event) of *P. fluviatilis* was significantly different between locations, more *P. fluviatilis* were collected outside (mean = 60.13) than inside (mean = 27.25) the MPA ($t_{11.413}$ = −3.86, *p* = .002, Table 1). *Rutilus rutilus* ($t_{11.129}$ = 3.06, *p* = .011) and *A. alburnus* (W = 64, *p* < .001) CPUEs were also significantly different; more fishes were collected inside (mean *R. rutilus* = 65.63, *A. alburnus* = 38.88) than outside (mean *R. rutilus* = 22.25, *A. alburnus* = 0) the MPA. Bream and *S. erythrophthalmus* abundance CPUE values were not significantly different among locations at a significance threshold of *p* ≤ .05 (Table 1). The biomass CPUE (total mass of fish species g/162 m² gillnet/location/sampling event) of *P. fluviatilis* (W = 6, *p* = .004) and *A. alburnus* (W = 64, *p* < .001) was also greater outside (mean *P. fluviatilis* = 6425.5 g, *A. alburnus* = 386.4 g) than inside (mean *P. fluviatilis* = 2031.9 g, *A. alburnus* = 0 g) the MPA. However, *R. rutilus*, *C. carassius* and *S. erythrophthalmus* biomass CPUE did not significantly differ among locations.

## 3.4 | Abiotic comparisons

Salinity, temperature and pH were not significantly different between locations. However, turbidity was higher outside (4.73

**TABLE 2** Parameter estimates and 95% confidence intervals (95% CI) obtained from bootstrapping (10,000 iterations), Akaike information criterion (AIC), Δ AIC, and AIC weight for the most parsimonious von Bertalanffy, logistic, and Gompertz growth models used to describe *P. fluviatilis* growth between locations inside (in) and outside (out) the marine-protected area (MPA)

| Growth between locations | | | | |
|---|---|---|---|---|
| Parameter | Estimate (95% CI) | AIC | Δ AIC | AIC weight |
| von Bertalanffy | | | | |
| $L_\infty$ – in | 685.86 (450.05 to 2002.74) | 6590.11 | 11.89 | 0.00 |
| $L_\infty$ – out | 305.81 (289.22 to 328.12) | | | |
| $K$ – in | 0.06 (0.02 to 0.11) | | | |
| $K$ – out | 0.26 (0.21 to 0.31) | | | |
| $t_0$ – in | −1.47 (−2.25 to −0.83) | | | |
| $t_0$ – out | −0.16 (-0.47 to 0.09) | | | |
| Logistic | | | | |
| $L_\infty$ – in | 358.44 (322.01 to 407.37) | 6578.22 | 0.00 | 0.65 |
| $L_\infty$ – out | 273.76 (265.88 to 282.35) | | | |
| $c$ – in/out | 3.92 (3.60 to 4.35) | | | |
| $g$ – in | 0.33 (0.28 to 0.40) | | | |
| $g$ – out | 0.61 (0.56 to 0.67) | | | |
| Gompertz | | | | |
| $L_\infty$ – in | 418.59 (356.01 to 532.34) | 6579.46 | 1.24 | 0.35 |
| $L_\infty$ – out | 284.20 (273.73 to 296.98) | | | |
| $g$ – in | 0.19 (0.14 to 0.25) | | | |
| $g$ – out | 0.43 (0.37 to 0.50) | | | |
| $t_0$ – in | 3.23 (2.41 to 4.83) | | | |
| $t_0$ – out | 1.46 (1.34 to 1.59) | | | |
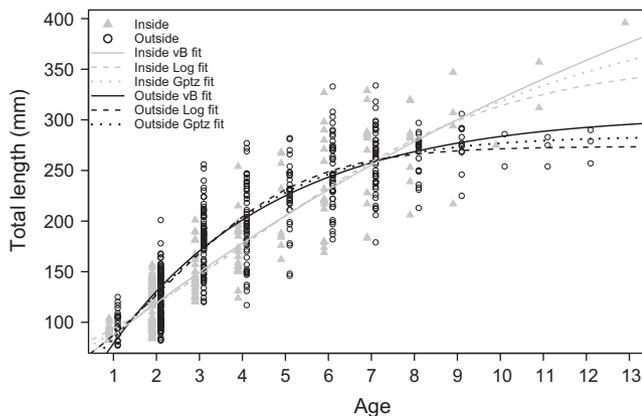


**FIGURE 5** Total length (TL) at age for *P. fluviatilis* collected inside (*n* = 222) and outside (*n* = 475) of the marine-protected area (MPA). The growth curve for each location is shown that was obtained from the most parsimonious von Bertalanffy (vB), logistic (Log), and Gompertz (Gptz) growth equations. The logistic curve was the best-fitting model among all types and all parameters were different between locations, except for the inflection point of the curve (*c*)

ntu) than inside (2.18 ntu) the MPA ($t_{7.91}$ = 5.24, *p* < .001). Mean parallel net depths were similar between locations, but perpendicular nets were on average 0.9 m deeper outside (3.8 m) than inside the MPA (2.9 m, $t_{12.902}$ = 2.21, *p* = .045). During every sampling event, SAV was present at both inside and outside

sites. This vegetation was dominated by mats of yellow–green filamentous algae, *Vaucheria litorea* Agardh, followed by milfoil (*Myriophyllum* sp.) in both locations. Fishing effort was also observed outside the MPA. Hook and line anglers were observed on four of the eight nights of sampling, and between two and six recreational gillnets were seen every night of sampling (Figure 1).

## 4 | DISCUSSION

### 4.1 | Condition, growth and species interactions

The condition of *P. fluviatilis* did not differ between locations. *Perca fluviatilis* collected outside of the MPA had a higher mean length (188 vs 158 mm), although mean weight of fish was not different between locations. This is atypical because fish inside MPA boundaries are expected to be longer than fish outside the MPA if fishing pressure is decreasing the average size of fish (Lester et al., 2009). Although fish were, on average, longer outside the MPA, the longest and heaviest fish were collected within the MPA, and all models predicted that fish inside the MPA should reach larger sizes than those outside (358 vs 274 mm, respectively).

All model types (vB, Log, Gptz) revealed minor sex-specific *P. fluviatilis* growth differences, and the best-fitting Gompertz model held all parameters equal between sexes except for the instantaneous rate of growth (*g*). Growth differences between fish

| | Abundance CPUE ± 1 *SE* | |
|---|---|---|
| **Species** | **Inside** | **Outside** |
| *Perca fluviatilis* | 27.25 ± 4.35 | 60.13 ± 7.31 |
| *Sander lucioperca* | 0.13 ± 0.13 | 1.13 ± 0.44 |
| *Esox lucius* | 1 ± 0.27 | 0.88 ± 0.40 |
| *Alburnus alburnus* | 38.88 ± 12.31 | 0 |
| Bream (*Blicca bjoerkna, Abramis brama,* and hybrids) | 24.63 ± 2.82 | 30.75 ± 4.46 |
| *Carassius carassius* | 0.75 ± .25 | 0.13 ± 0.13 |
| *Clupea harengus* | 0.88 ± 0.40 | 0 |
| *Rutilus rutilus* | 65.63 ± 12.30 | 22.25 ± 7.02 |
| *Scardinius erythrophthalmus* | 3.88 ± 1.26 | 0.88 ± 0.40 |
| *Gymnocephalus cernuus* | 0.5 ± 0.27 | 2.63 ± 0.53 |
| *Tinca tinca* | 0.13 ± 0.13 | 0 |
| *Coregonus lavaretus* | 0 | 0.13 ± 0.13 |
| | Biomass (g) CPUE ± 1 *SE* | |
| *Perca fluviatilis* | 2031.94 ± 429.09 | 6425.50 ± 1217.06 |
| *Sander lucioperca* | 5.71 ± 5.71 | 167.93 ± 87.49 |
| *Alburnus alburnus* | 386.35 ± 121.60 | 0 |
| Bream (*Blicca bjoerkna, Abramis brama,* and hybrids) | 655.48 ± 138.78 | 1919.88 ± 300.50 |
| *Carassius carassius* | 321.86 ± 147.63 | 118.75 ± 118.75 |
| *Clupea harengus* | 13.49 ± 6.14 | 0 |
| *Rutilus rutilus* | 2067.13 ± 428.81 | 1163.54 ± 429.52 |
| *Scardinius erythrophthalmus* | 300.16 ± 90.15 | 451.93 ± 226.35 |
| *Gymnocephalus cernuus* | 6.44 ± 3.53 | 21.04 ± 3.63 |
| *Tinca tinca* | 125 ± 125 | 0 |
| *Coregonus lavaretus* | 0 | 1.6 ± 1.6 |

**TABLE 3** Abundance CPUE (number of fish/162 m$^2$ gillnet/location/sampling event) ± 1 standard error (*SE*) and Biomass CPUE (total mass of species (g)/162 m$^2$ gillnet/location/sampling event) ± 1 *SE* of fishes collected inside and outside the Husö marine-protected area (MPA). *E. lucius* were released in the field at their collection location; therefore, no biomass values were obtained inside or outside the MPA

collected inside and outside of the MPA were large. The logistic model was the most parsimonious, with all parameters differing by location, except for the inflection point of the curve (*c*). All model types were similar and predicted a higher $L_\infty$ value for fish inside the MPA, therefore, fish were predicted to grow larger within the MPA. Fish outside the MPA were predicted to grow faster early in life, but be smaller after age-7, given the lower $L_\infty$ value for this location. This explains why mean fish length was higher outside the MPA, because most fish collected were younger than 7 years. This age-7 length shift, along with the large $L_\infty$ for inside fish, implies that the largest fish should be found inside the MPA, and such was the case; although, the sample size of large fish was limited. Theoretically, if more fish over age-7 had been collected, it is possible that mean fish length would have been greater inside the MPA.

The difference in growth between the two populations may be a result of changes due to recreational fishing pressure, differences in species interactions between the two locations, or other environmental drivers that were not detectable. Fishing has been shown to decrease the overall size of fish, and affect growth and maturation,

and the majority of growth effects have been attributed to changes in maturation (Heino, Díaz Pauli & Dieckmann, 2015; Lewin et al., 2006). When fish harvest occurs, fished populations have been shown to respond with increased growth in the juvenile phase, permitting them to reach maturity sooner than in unfished populations (Heino et al., 2015; Lewin et al., 2006; Trippel, 1995). Once maturity is attained, more energy is allocated to gonad growth instead of somatic growth, resulting in decreased overall fish size (Roff, 1983). This type of response has been found in recreationally exploited fishes (Coleman et al., 2004; Diana, 1983; Drake, Claussen, Philipp & Pereira, 1997; Lewin et al., 2006) and was potentially documented in a population of exploited *P. fluviatilis* in Estonia (Pukk, Kuparinen, Järv, Gross & Vasemägi, 2013). Following exploitation, fish were shown to have decreased age and length, an increase in juvenile growth rate, and earlier maturation in male fish, although these effects may be attributable to immigration of fish from other populations (Pukk et al., 2013). In this study, differences in GSI between locations were not detected and maturation was not studied. Although, the differences in modelled growth inside and outside of the MPA (specifically, faster juvenile growth with decreased overall

sizes outside of the MPA) suggest that a fishery-induced effect on growth may be occurring. However, there are some findings that fit less with fisheries-induced growth changes. One of the major pieces of data that refutes this is the larger mean size and catch of *P. fluviatilis* captured outside of the MPA (Hilborn et al., 2004). This presents a discord where, at least currently, fisheries-induced changes to the size and age distribution are not obvious. It is possible that in the past, higher levels of exploitation may have driven the currently observed growth pattern. Further investigation on the effects of fisheries-induced life history changes in *P. fluviatilis* is needed.

Another mechanism that may have resulted in the growth differences observed in this study is the community differences between the two locations. The higher density of *R. rutilus* and *A. alburnus* inside the MPA, coupled with the higher density of *P. fluviatilis* outside the MPA, could result in the growth differences observed in this study, given complex interspecific and intraspecific interactions (Persson, 1983a,b; Persson & Greenberg, 1990). Inside the MPA, young *P. fluviatilis* may compete with *R. rutilus* for zooplankton, given that this interspecific competition has been found before (Persson, 1983a). This interaction has resulted in *P. fluviatilis* switching from zooplankton to benthic invertebrate prey, decreasing their growth rate (Persson, 1987; Persson & Greenberg, 1990), and potentially decreasing numbers of young *P. fluviatilis* (Persson, 1983a, 1986). These interactions could explain the slower growth of young *P. fluviatilis* and the sharp decline in *P. fluviatilis* after age two inside the MPA. This decrease in fish older than two could lead to less intraspecific competition (Persson, 1983b), thus allowing the remaining *P. fluviatilis* to grow unhindered inside the MPA, albeit slower than outside while young, given the benthic invertebrate prey switch (Persson, 1987; Persson & Greenberg, 1990). Once *P. fluviatilis* inside the MPA become piscivorous, it is probable that the abundant *R. rutilus* and *A. alburnus* provide bountiful food resources (Eklov & Persson, 1995; Persson, Diehl, Johansson, Andersson & Hamrin, 1992), allowing the *P. fluviatilis* remaining inside the MPA to reach the large sizes predicted by the growth models.

Outside the MPA, the opposite mechanism could be occurring and intraspecific competition between *P. fluviatilis* may be of more importance, especially at larger sizes. For instance, when *P. fluviatilis* are zooplanktivorous, they may be able to feed unhindered, given the lower abundances of cyprinids (Persson, 1983a, 1986; Persson & Greenberg, 1990). This could result in the increased juvenile growth rate (Persson, 1987) observed outside the MPA. However, after the piscivorous stage is reached, intraspecific competition (Persson, 1983b), coupled with fewer cyprinid prey, could result in decreased growth of large *P. fluviatilis*, producing the smaller $L_\infty$ predicted for this location.

In addition to fisheries-induced changes and ecological interactions, the observed differences in growth inside and outside of the MPA may be due to environmental or genetic differences that were not detected by the sampling. Pukk et al. (2013) indicated that *P. fluviatilis* likely has locally adapted gene complexes that affect growth.

It is possible that the observed differences in growth between the two locations are at least partially due to genetically encoded differences that may be a result of local adaptation to one or more environmental or ecological factors that differ between the sampling locations (Kawecki & Ebert, 2004). Genomic or transcriptomic work as well as correlations between environmental, phenotypic or ecological data would be needed to disentangle any genetic effects that may be at play. There may also be direct environmental or habitat differences affecting *P. fluviatilis* growth that were not observed during this study. Differences in density of aquatic vegetation can affect the survival and growth rate of *P. fluviatilis*, given the prey refuge provided by structurally complex habitats (Diehl, 1988; Diehl, 1993; Persson & Eklov, 1995). *Perca fluviatilis* growth could be affected by basin depth and size, because basin morphology affects fish community structure and abiotic factors in the Baltic (Snickars et al., 2005, 2009). Productivity differences among locations may also drive some of the community and growth differences (Adjers et al., 2006; Mustamäki & Mattila, 2015; Persson et al., 1992) observed in this study.

## 4.2 | Community structure

Two of the potential benefits of MPAs are higher species richness and intact community structure. These advantages are attributed to both habitat protection and higher densities of fished species (Claudet et al., 2008; Halpern & Warner, 2003; Lester et al., 2009). This study follows this trend in that the fish community within the MPA was more diverse than the fish community outside the MPA (11 vs 9 species, respectively), although this could also be due to environmental differences between the two locations. The main species abundance differences between locations involved higher numbers of *P. fluviatilis* outside of the MPA, and higher numbers of *R. rutilus* and *A. alburnus* inside the MPA. As discussed in the previous section, these differences could be affecting *P. fluviatilis* growth at both locations, given interspecific and intraspecific interactions. Elevated abundance of the popular recreational fish *P. fluviatilis* outside of the MPA was unexpected, as fishing should decrease the numbers of targeted fish outside of the MPA (Lewin et al., 2006; Westera et al., 2003).

The higher density of *P. fluviatilis* outside of the MPA may be explained by unavoidable habitat differences between the two locations. The sites sampled outside of the MPA were somewhat less enclosed and were surrounded by deeper waters, although this difference was only slight, as demonstrated by the perpendicular net depths. Deeper areas may harbour increased numbers of *P. fluviatilis*, as these fish have been shown to move to deeper waters following spawning (Saulamo & Neuman, 2002). This suggests that exchange of adult fish may be occurring between the MPA and outside sites (Sundblad et al., 2011, 2014). In mark–recapture experiments in coastal waters of Finland and Estonia, the majority of *P. fluviatilis* moved about 10 km (Böhling & Lehtonen, 1985; Järv, 2000), although some perch travelled as far as 150 km (Järv, 2000). The question of whether significant fish exchange is occurring between

MPAs and harvestable locations is inherent for determination of MPA effectiveness (Botsford et al., 2009; Grüss, Kaplan, Guénette, Roberts & Botsford, 2011; Hilborn et al., 2004). In the Åland system, further work needs to be conducted to answer this question, given that fish behaviour and movement distances could be different in this system, and this information is imperative for MPA assessment. A mark–recapture study with external tags, as well as a telemetry study, could elucidate fish movement between protected and unprotected waters.

It is also possible that even if physical movement of fishes is occurring between locations, there could still be genetic isolation between *P. fluviatilis* populations. Genetic differentiation has been found among samples collected from different basins along the Gulf of Bothnia (Pukk et al., 2013). When sampling was expanded to larger areas of the Baltic, within-region (e.g. Western Estonia) differentiation deteriorated, but among-region (e.g. Finland vs Estonia) differentiation remained high (Pukk, Gross, Vetemaa & Vasemägi, 2016). A low level of genetic connectivity has also been found in the Baltic between adjacent locations without physical barriers to dispersal, indicating a lack of exchange between local demes (Olsson, Mo, Florin, Aho & Ryman, 2011). Lastly, the growth differences observed between locations indicate that demographically significant exchange is not likely occurring. A genetic comparison between fish from inside and outside the MPA would be of interest to determine whether there is differentiation between locations, such as distinct spawning populations.

It is difficult to disentangle fishing and other environmental effects on fish growth and this is the main reason why field-based evidence of fishery-induced effects is difficult to produce (Heino et al., 2015). It is likely that *P. fluviatilis* growth differences between locations inside and outside the MPA are a combination of fishery-induced effects, differences in species interactions between locations and other environmental variation that could not be quantified. The numbers and sizes of *P. fluviatilis* collected outside of the MPA do not indicate that the fishery is in poor condition. However, to determine whether the MPAs in the Åland Islands are effectively protecting *P. fluviatilis* and other fishes from recreational exploitation, future work should strive to pinpoint what mechanisms are driving the growth differences observed in this study; given that these growth differences may provide field-based evidence of fishery-induced effects, as well as overall MPA effectiveness. Future work should also replicate these growth and community comparisons among other MPA and harvested locations within the Åland Islands. Mark–recapture studies using traditional and telemetry tags would be beneficial to investigate fish exchange between protected and non-protected areas (Farmer & Ault, 2011; Kerwath et al., 2009; Meyer, Papastamatiou & Clark, 2010) and could provide estimates of mortality and population sizes (Pine, Pollock, Hightower, Kwak & Rice, 2003). Furthermore, genetic and otolith chemistry studies could help to elucidate population connectivity and sources of fish among protected and non-protected areas

(Di Franco et al., 2012; Engstedt, Stenroth, Larsson, Ljunggren & Elfman, 2010; Pukk et al., 2013, 2016). Finally, productivity, habitat and diet comparisons among locations investigated in this study could explain why fish communities differ and if the competitive interaction mechanisms described above are occurring. These future studies would help to elucidate whether fishing or other environmental variables are driving the observed growth differences in *P. fluviatilis* between locations inside and outside of a MPA and if growth differences are widespread between protected and fishing areas in the Baltic Sea.

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