Journal of
Molluscan Studies

The Malacological Society of London

*Journal of Molluscan Studies* (2025) **91**: eyaf003. https://doi.org/10.1093/mollus/eyaf003

# Estimating a length-at-age relationship for an invasive bivalve with density-determined plastic growth

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(Received 18 October 2023; editorial decision 11 March 2025)

## ABSTRACT

At the base of stock assessments, used to monitor invasive aquatic species and to sustainably harvest stocks, are estimates of body growth, a key parameter regulating animal populations. However, due to lack of data, obtaining these estimates can be challenging, but analytical approaches for 'data-poor' situations have been developed. Currently, the Pacific oyster (*Magallana gigas*) is spreading in northern Europe and a need for management strategies to control the invasion is evident. Using methods developed for data-poor situations, the von Bertalanffy growth function and electronic length-frequency analysis, we analysed 17,289 length measurements of wild Pacific oysters collected between 2007 and 2018 at five sites in Sweden to estimate its growth in temperate waters. We identified two distinct growth patterns, where individuals in habitats with high bivalve density grow faster in length compared to those in less dense habitats. Additionally, we found that Pacific oyster populations in Sweden are still growing towards their asymptotic lengths and that growth is reduced but not stopped during colder months. We conclude that our analysis constitutes the basis for future stock assessment and management of the species in areas with feral populations of commercial interest.

## INTRODUCTION

Estimates of body growth in fish and aquatic invertebrate populations provide information regarding life-history traits and form the base of many stock assessments (Lorenzen, 2016; Schwamborn, Mildenberger & Taylor, 2019). Stock assessment models are primarily used to sustainably manage commercially exploited populations (Pauly & David, 1981; Methot Jr. & Wetzel, 2013), but they also allow for the monitoring of invasions, such as the case of the rapa whelk (*Rapana venosa*) in the Black Sea (GFCM, 2022).

Several challenges are associated with the estimation of body growth for stock assessments. First, depending on the study species, different biological data can be collected for this purpose, such as tagging-recapture data and periodic markings on scales, otoliths and skeletons (Pauly & David, 1981). However, due to logistic difficulties and expensive field work associated with the collection of these data, many fisheries are referred to as 'data-poor', meaning that only size-frequency (e.g. catch, length and weight) data are available, and where little is known about the dynamics of specific exploited populations (Dowling *et al.*, 2015). A second challenge is the notion of phenotypic plasticity in growth. Plastic growth patterns vary in response to biotic and abiotic factors (Brett, 1979), where the phenotype expressed changes depending on the conditions at different spatial locations, the time of year, and impacts of metapopulations (Kritzer & Davies, 2005; Pigliucci, Murren & Schlichting, 2006; Nussey, Wilson & Brommer, 2007). As a result, growth patterns of populations of the same species, and even separate components of the same stock, can vary over time and across locations. Furthermore, plastic growth patterns can affect the size structure of a population as well as its dynamics and productivity (Stearns & Koella, 1986; Heino, Dieckmann & Godø, 2002).

Analytical approaches have been developed for data-poor situations, where size-frequency data can be used to model growth. Several length-structured methods for estimating growth are available, where the most common is the fitting of growth curves to length-at-age data. The von Bertalanffy growth function (von Bertalanffy, 1938) is routinely used for this purpose since it is known to conform to the growth pattern of many fish and aquatic invertebrate species (Gosling, 2007; Mildenberger, 2017). The von Bertalanffy growth function assumes that growth is rapid during the first few years, slows down over time and levels off at older ages (von Bertalanffy, 1938). Additionally, the von Bertalanffy growth function captures some aspects of phenotypic plasticity through its considerations of seasonal effects on growth (Somers, 1988), bioenergetics and scaling relationships (von Bertalanffy, 1938; Lorenzen, 2016). The standard approach to estimate growth parameters from length-frequency data is through electronic length-frequency analysis (ELEFAN; Pauly, 1980, 1987; Pauly & David, 1981; Gayanilo & Pauly, 1997). Several packages for the statistical environment R, such as TropfishR (Mildenberger, Taylor & Wolff, 2017a, b; Mildenberger, 2017) and fishboot (Schwamborn, Mildenberger & Taylor, 2018), allow for more functionality of the ELEFAN compared to older software (i.e. FiSAT II; Gayanilo *et al.*, 1996).

The Pacific oyster *Magallana gigas* (Thunberg, 1793), previously part of the genus *Crassostrea* but moved to the genus *Magallana* in 2017 by Salvi & Moariottini (2017, 2021), is one of the worlds' most successful invasive species, largely due to its popularity within the aquaculture industry (Wrange *et al.*, 2010; Strand & Lindegarth, 2014; Laugen *et al.*, 2015). The species was first introduced to Scandinavia through cultivation in Denmark in the 1970s and cultivation trials in Sweden between 1973 and 1976. The trials in Sweden concluded that cultivation was possible; however, no spawning and no natural recruitment was observed (Ekelund, Håkansson & Haamer, 1977). After production was discontinued in Denmark in the 1990s, the oysters were abandoned with the belief that the cold waters of the North Sea would be too stressful for their physiology (Wrange *et al.*, 2010). However, the Pacific oyster has thereafter established permanent populations in all countries of Scandinavia. In Sweden, the species was first sighted in 2007 (Wrange *et al.*, 2010) and by 2014, more than 250 locations with Pacific oyster populations containing a total biomass between 100,000 and 500,000 tons have been identified along the northern Swedish west coast (Strand & Lindegarth, 2014).

The European framework for the mitigation of alien species (EU regulation no. 1143/2014) incorporates management strategies for the prevention, early detection and rapid eradication of an invasive species. The Pacific oyster has been present in northern Europe for *c.* 15 years and the established populations are no longer feasible to eradicate (Mortensen *et al.*, 2019, 2022). Additionally, densities of Pacific oysters are expected to increase at already colonized sites and the species is predicted to disperse further north in Scandinavia, along the Norwegian coast (Wrange *et al.*, 2010; Dolmer *et al.*, 2014; Strand & Lindegarth, 2014; Laugen *et al.*, 2015). At the time of writing, no management strategy to control the Pacific oyster invasion is in place in Scandinavia and the approach has been to accept the species as an integrated part of the marine ecosystem (Mortensen *et al.*, 2022). However, due to its potential negative impacts on native species (Nehls *et al.*, 2006; Troost *et al.*, 2009) and recreational activities (Mortensen *et al.*, 2022), there is a need to monitor its dispersal. A strategy under consideration involves developing a monitoring programme to detect expanding local populations and to identify where site-specific efforts, such as manual removal, can be implemented to avoid dispersal to new areas (Dolmer *et al.*, 2014). Additionally, since the Pacific oyster is an important aquaculture species, there is a growing interest in harvesting the populations both to control the invasion (Mortensen *et al.*, 2019, 2022) and to create a benefit for local economies.

Since the settlement of the Pacific oyster in Sweden in 2007, length-frequency measurements of individual oysters and site-specific densities have been collected on a yearly basis from five locations on the Swedish west coast, a core area of the invasion. As a result, we have access to a time series of length-measurements and densities from wild oysters over an 11-year period (2007–2018, excluding 2012). This time series provides an excellent opportunity to estimate the growth rate of the Pacific oysters at these five locations and to test the applicability of statistical tools developed for data-poor fish stocks, including functions in R packages TropfishR and fishboot. Furthermore, it allows us to apply the methods to a species that has displayed a plastic growth pattern (Nehring, 2011), which presents an additional difficulty when analysing length-frequency distributions for estimating growth. In particular, Pacific oysters that share habitat with many other bivalves, in areas where competition for food and space is likely to be high, will mostly grow long and narrow, while individuals that live in areas with low bivalve density will mostly grow shorter and wider (Dolmer *et al.*, 2014; Strand & Lindegarth, 2014). The aims of this study were, therefore, to (1) model the growth of Pacific oysters in Sweden and establish a length-at-age relationship, (2) investigate heterogeneity in growth and density across populations to understand the importance of site-specific management strategies and (3) to test the applicability of ELEFAN to wild Pacific oysters with a plastic growth pattern. By estimating the growth rate of wild Pacific oyster populations through length-at-age relationships, we can use the information as the basis for future management and stock assessments of the species.

## MATERIAL AND METHODS

### *Study area*

Throughout 11 years of data collection (2007–2018, excluding 2012), five locations along the Swedish west coast have been sampled mostly during the northern hemisphere summer (June–August) and occasionally during spring (May) and autumn (October) (Fig. 1).

### *Data collection*

At each sample location, an outer perimeter of the oyster population was first established by using an aquascope. This outer perimeter was, for practical reasons, determined as either where the water became too deep for sampling (>0.8 m) or where the oysters could no longer be seen and, thus, were assumed to be absent. Second, two to three transects were laid parallel or perpendicular to the shore to capture a wide range of oyster lengths and densities at varying depths. A quadrat of 0.5 × 0.5 m was used with a 1-m interval along the transect lines. The quadrat was placed on the bottom and all oysters within the square were measured to the nearest 1.0 mm with a Vernier calliper from the umbo to the outer edge of the shell (the maximum outer shell length) (Fig. 2; Table 1). At locations where the oyster density was higher, a 0.25 × 0.25 m quadrat was used and placed on the bottom at 2-m intervals. After being measured, each oyster was returned to the water close to the quadrat to avoid changing the natural composition of the population. Additionally, oyster density was measured as the number of individuals per $m^2$ for each site and year.

### *Electronic length-frequency analysis*

ELEFAN was first described by Pauly & David (1981) and comprises several analytical steps, in which the first procedure involves fitting growth model parameters from the progression of length-frequency modes through time. This procedure uses the logarithmic von Bertalanffy growth function to convert length-frequency data into age composition by expressing the length of the organism ($L$) as a function of its age ($t$)

$$L_{(t)} = L_\infty \left(1 - e^{-K(t-t0)}\right)$$

where $L_\infty$ is the average asymptotic length; $K$ is the growth constant, which estimates the exponential rate of how fast the population is approaching $L_\infty$ year$^{-1}$ (curvature parameter); and $t_0$ is the hypothetical age when the organism has zero length (initial condition parameter).

However, Pacific oysters follow a seasonal growth pattern due to annual fluctuations of environmental factors (Gagnery *et al.*, 2003; Diederich, 2006; Cardoso *et al.*, 2007; Pogoda, Buck & Hagen,

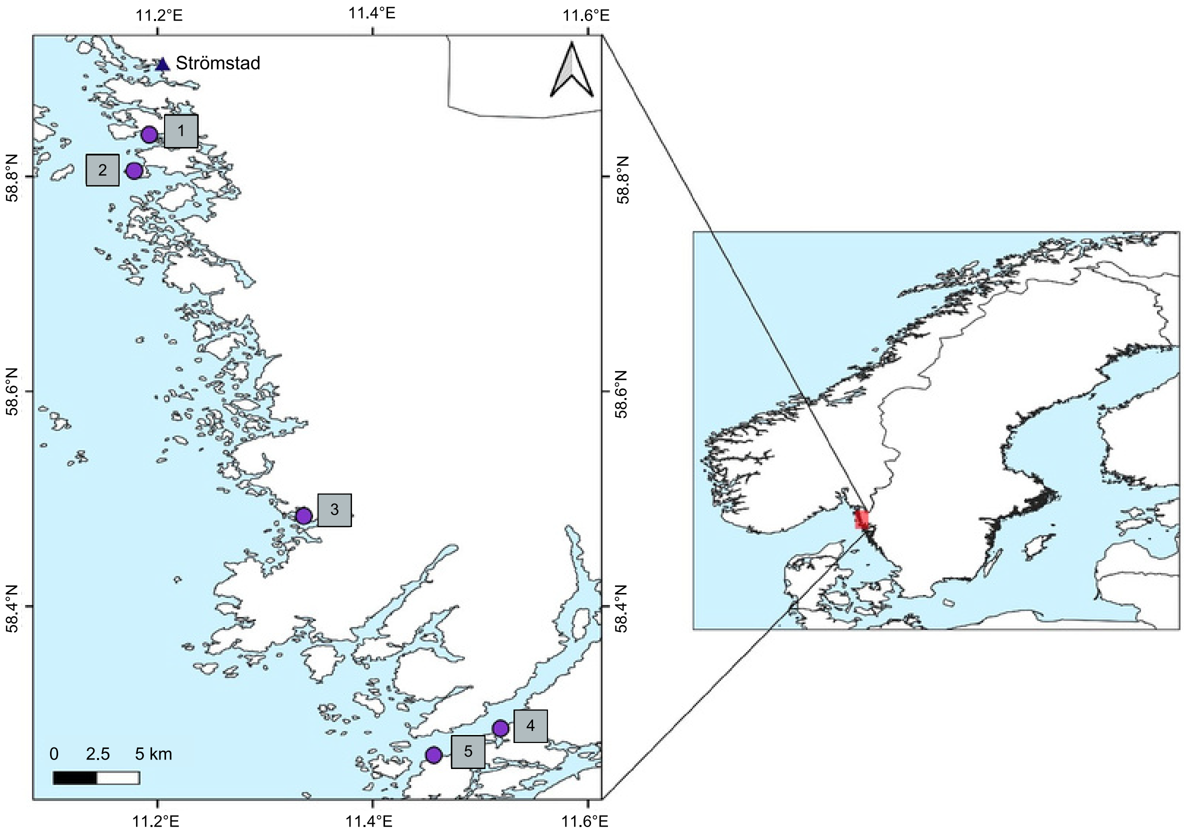

**Figure 1.** Five data collection points on the northern Swedish west coast. Site names: (1) Svallhagen, (2) Kockholmen, (3) Sältången, (4) Getevik and (5) Smalsundet. The distance between Svallhagen and Smalsundet is roughly 39.2 km. Sites were sampled between 2007 and 2018 (excluding 2012).

2011; Góngora-Gómez *et al.*, 2017). It is therefore important to analyse the growth of Pacific oysters under these conditions. By incorporating a sine curve with a wavelength of 1 year, we can fit a seasonally oscillating von Bertalanffy growth function (Somers, 1988)

$$L_{(t)} = L_{\infty}\left\{1 - e^{-(k(t-t0)\,+S(t)-\,S(t0))}\right\}$$

$$\text{with } S_{(t)} = \left(\frac{CK}{2\pi}\right)\sin\left(2\pi\left(t - t_s\right)\right)$$

$$\text{so } S_{(t0)} = \left(\frac{CK}{2\pi}\right)\sin\left(2\pi\left(t_0 - t_s\right)\right)$$

where the parameter $t_s$ determines the time of year, relative to the age of recruitment ($t = 0$), where the first sinusoidal oscillation begins, and the parameter $C$ sets the amplitude of the decrease in growth at the depth of the growth oscillation (referred to as the 'winter point'). At the winter point, the increase in mean length of an organism can be completely halted ($C = 1$), unaffected ($C = 0$) or reduced, but not stopped ($0 < C < 1$). If $C > 1$, the organism is assumed to be shrinking. However, annual shrinkage is unlikely for most organisms (Pauly & Gaschütz, 1979) and length loss due to wear and tear of oyster shells is, most likely, lower than the annual growth. Therefore, $C = 1$ has been proposed as the upper limit for this parameter.

### *Electronic length frequency analysis using R*

The R-packages TropfishR (Mildenberger *et al.*, 2017a, b; Mildenberger, 2017) and fishboot (Schwamborn *et al.*, 2018) offer single-species stock assessments, including electronic length-frequency analysis, and a straightforward incorporation of potential seasonal changes in growth (Supplementary Material Fig. S1 illustrates the procedures below for readers unfamiliar with this analysis). Furthermore, fishboot provides confidence limits around the growth estimates, which were not provided by older software (Schwamborn *et al.*, 2019).

To estimate Pacific oyster growth curves, we used TropfishR and fishboot in R v. 3.6.3 (R Core Team, 2024). The growth estimation is done in four distinct steps: the first three use TropfishR and the fourth uses fishboot. The first step transforms individual length measurements of the study population(s) into length-frequency data. The second step identifies cohorts that can be traced through time. To restructure the length-frequency data generated in the previous step, scores are assigned to intervals of length-frequencies dependent on their deviation from a moving average. The size of the length interval (bin size) is then divided by the moving average. The bin size and the value for the moving average are selected by the user and we detail the choices we made for our model system in the next section. The third step involves selecting settings for a seasonally oscillating von Bertalanffy growth function, and the parameter values we chose for this model system are also detailed in the section below (Parameterization). The fourth and last step is fitting growth curves through the cohorts of the restructured length-frequency data until the curves with the highest score and the 'best' parameter combinations of the seasonally oscillating growth function have been identified using bootstrapped functions from the fishboot package. These bootstrapped versions of the ELEFAN functions resample data with replacement to obtain uncertainty estimates around the predicted growth curves. See the section Performance of growth curves below for details.

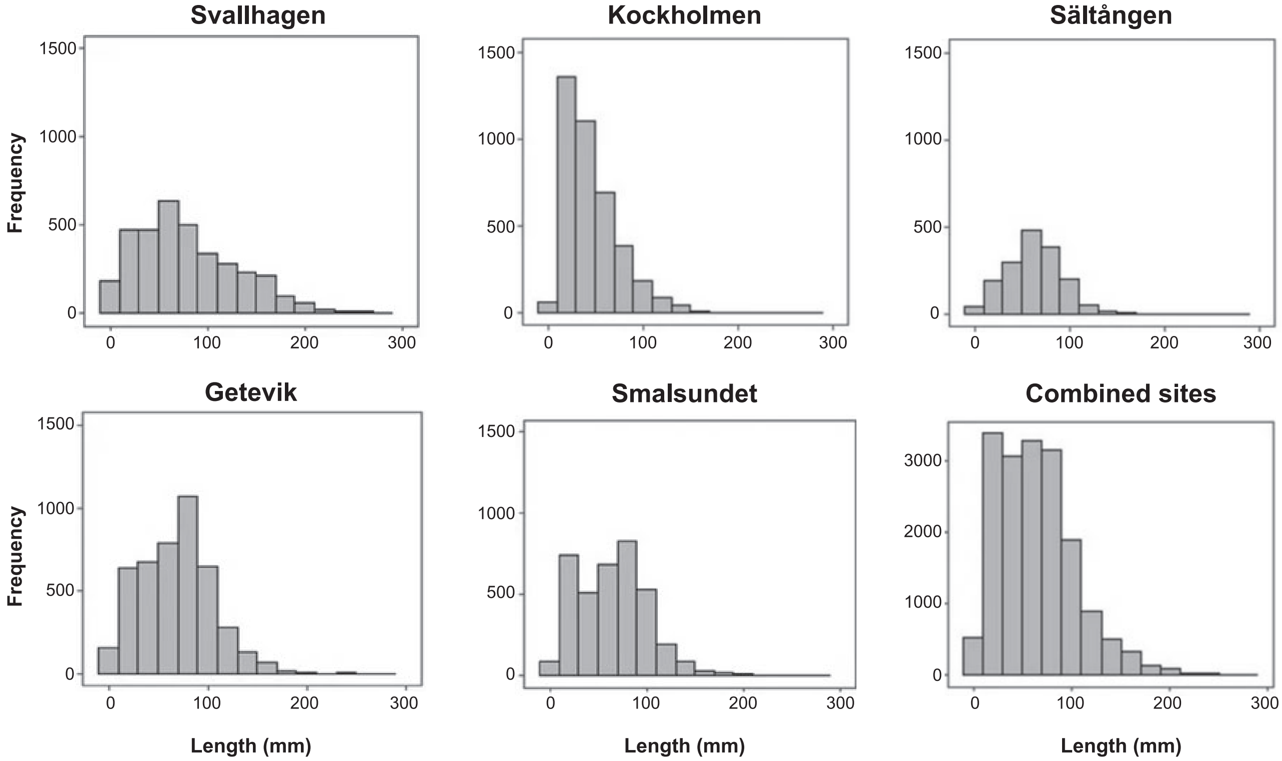

**Figure 2.** Shell length-frequencies of Pacific oysters for each sampling location and pooled across sites from a time series of data collected along the northern part of the Swedish west coast (2007–2018, excluding 2012). Note that the limit on the *y*-axis is 1,500 observations for the individual sites and 3,500 observations for the combined data.

**Table 1.** Sampling sites, sample sizes, measured shell lengths (minimum, median and maximum lengths in mm), parameters for estimating cohorts and starting parameters for a seasonally oscillating von Bertalanffy growth model, from a study of shell growth of the invasive Pacific oyster on the Swedish west coast (sampled 2007–2018, except 2012).

| | Empirical shell lengths (mm) | | | | Cohort definition* | | von Bertalanffy growth model parameters$^+$ | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site | *N* | Min. | Med. | Max. | Bin | MA | Lwr | Upr | *K* | *t_anchor* | *C* | $t_s$ |
| **Svallhagen** | 3,492 | 1 | 70 | 275 | 10 | 5, 7, 9 | 137.5 | 400 | 0.01–1.00 | 0.50–0.75 | 0–1 | 0–1 |
| **Kockholmen** | 3,925 | 1 | 39 | 231 | 10 | | 115.5 | | | | | |
| **Sältången** | 1,667 | 1 | 63 | 177 | 10 | | 88.5 | | | | | |
| **Getevik** | 4,487 | 3 | 70 | 250 | 15 | | 125 | | | | | |
| **Smalsundet** | 3,718 | 4 | 67 | 240 | 10 | | 120 | | | | | |

∗Cohort definitions: bin, width of the interval of length–frequency data; MA, values for the moving average applied to the length frequency data for cohort definition.
+Model parameters: lower (Lwr) and upper (Upr) limits for the asymptotic length; *K*, growth constant ($K$ year$^{-1}$); *t*, time of year that the oysters settle; *C*, amplitude of the growth oscillation; and *ts*, time of year that the growth turns positive after the winter point.

We estimated Pacific oyster growth in two different sets of analyses to explore whether there was strong evidence of site-specific growth patterns. First, we combined the data, assuming a homogeneous growth pattern across all five sites. Then, to allow differences in growth between sites to exert an effect, we ran separate models for each of the five locations. During the reconstruction of the length-frequency data, the choice of length intervals was based on the proposed method by Wolf (1989), where the length of the largest individual in each sample is divided by the number of modal groups assumed to be present at each site. For three of our sites, Kockholmen, Smalsundet and Sältången, we used a bin size of 10 mm, while for Getevik, Svallhagen and the combined sites, we used a bin width of 15 mm (Table 1). The moving average was selected on the rule of thumb developed by Taylor & Mildenberger (2017), where the chosen value should approximate the number of bins spanning the youngest cohort width. All samples identified the optimal moving average as 5. However, in their sensitivity analysis, Taylor & Mildenberger (2017) found that higher moving average settings in the TropfishR package resulted in growth curves with better fits. Therefore, we tested moving averages of 5, 7 and 9 (Table 1). Last, the fishboot package provides two 'optimization' calculations for fitting the von Bertalanffy growth function (ELEFAN_SA_boot, based on a generalized simulated annealing and ELEFAN_GA_boot, based on a genetic algorithm). Both functions allow for the incorporation of seasonal growth parameters and a simultaneous search for the seasonally oscillating von Bertalanffy growth function parameter combinations within the same state space. To increase the

**Table 2.** Length-at-age relationships (mm) at four age stages for the Pacific oyster and the estimated coefficients for the von Bertalanffy growth parameters.

| | Length-at-age relationships | | | | Estimated coefficients for the von Bertalanffy growth parameters | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Site | Age 1 | Age 3 | Age 5 | Age 11 | *L* | *K* | *t_anchor* | *C* | $t_s$ | Rn score |
| **Svallhagen** | 15 | 100 | 165 | 270 | 354.0 | 0.14 | 0.73 | 0.70 | 0.60 | 0.16 |
| **Kockholmen** | 15 | 70 | 115 | 200 | 284.2 | 0.12 | 0.71 | 0.79 | 0.60 | 0.22 |
| **Sältången** | 10 | 60 | 110 | 190 | 281.9 | 0.11 | 0.71 | 0.66 | 0.50 | 0.22 |
| **Getevik** | 15 | 120 | 180 | 250 | 266.7 | 0.27 | 0.70 | 0.77 | 0.50 | 0.17 |
| **Smalsundet** | 15 | 60 | 100 | 195 | 375.3 | 0.07 | 0.69 | 0.65 | 0.69 | 0.19 |
| **Combined sites** | 70 | 190 | 250 | 295 | 297.8 | 0.38 | 0.54 | 0.76 | 0.64 | 0.15 |

likelihood of obtaining optimal growth curves, we ran both optimization functions, each with a moving average setting of 5, 7 and 9. In total, six analyses were run for each of the five study sites and for the combined data (36 in total). Additionally, we used bootstrapping to assess uncertainty in the fitted curves. This procedure samples data using replacement and can therefore help ascertain the extent to which parameters may depend on the inclusion of rare observations.

### *Parameterization*

The initial step when running ELEFAN with fishboot is to specify input values for the five parameters of the seasonally oscillating von Bertalanffy growth function. These parameters are the asymptotic length ($L_\infty$), the growth constant (*K*), the time of year that the oysters settle (*t_anchor*, 'anchor time', used by fishboot instead of $t_0$), the amplitude of the growth oscillation (*C*), and the time of year that the growth turns positive after the winter point ($t_s$) (Table 1). Note that the seasonally oscillating von Bertalanffy growth function in the fishboot package uses age instead of time as in the traditional equation (Schwamborn *et al.*, 2018). If prior knowledge of the life history parameters of the study population is available, this can be used to provide a more specific and targeted analysis. For the Pacific oyster, the parameter for the time of year that the species settles in Sweden (*t_anchor*) was known prior to the analysis.

*t_anchor*: Previous studies show that most Pacific oysters settle in Sweden between middle to late August (Strand & Lindegarth, 2014), and the parameter *t_anchor* was therefore given a search range between the 1 July and the 1 October (0.5–0.75; Table 2). An additional month was added to the search range to cover a larger parameter space.

*K*: Since we do not know how fast the population grows towards the asymptotic length, the growth constant was given a wide search range between 0 and 1.

*C* and $t_s$: The impacts of season on the growth of the Pacific oyster populations were also unknown and these parameters were given their full search ranges (0–1).

$L_\infty$: Most commonly, it is recommended to fix the asymptotic length prior to the analysis (Gayanilo, Sparre & Pauly, 1996; Sparre & Vanema, 1998; Taylor & Mildenberger, 2017), often by using the largest individual in the sample. However, this approach has been criticized as it increases the risk of underestimating the maximum size of the oysters by assuming a relationship *a priori* between the largest individual in a sample and the maximum length of the population (Schwamborn, 2018; Schwamborn *et al.*, 2019). To avoid a search range too narrow for the asymptotic length for the Pacific oysters in Sweden, the lower limit was set as half the size of the maximum length of the oysters at each site and the upper limit was based on the historically largest record of a Pacific oyster, 400 mm (Nehring, 2011).

In total, 200 bootstrapped runs were performed for each of the 36 growth estimations and the curve with the best parameter combinations was identified through maximum density (i.e. the combination of values that was selected most often by the model). Furthermore, the performance of each curve was assessed by its ability to capture the growth pattern in the reconstructed length-frequency data.

## RESULTS

In total, more than 3,000 oyster length measurements were analysed for each of the study sites (except Sältången with 1,677) and the combined site data included 17,289 observations (Table 1). Most of the oysters were found within a size range of 5–100 mm (Fig. 2), where the largest oyster measured 275 mm and was found at site Svallhagen. The median oyster length ranged between 61 and 70 mm, except at site Kockholmen, which had a median length of 39 mm. Out of the 17,289 observations, only 85 individuals were longer than 200 mm and 67 of these were found at Svallhagen. In contrast, no individuals larger than 200 mm were recorded at Sältången.

### *Growth curves*

Out of the 36 analyses, 29 growth curves were rejected based on (1) having growth patterns that indicated that the oysters were limited to a maximum length far below the size of the largest individual at the site in question or (2) indicating that the largest oysters at each site were very young (≤7 years) (i.e. the curve estimated a very fast growth rate). Since the Pacific oysters settled in Sweden in 2007, we know that the largest oysters were at least 11 years old in 2018. An average age of 7 years or less for the largest individuals was, therefore, not biologically plausible in our study. In addition, the ELEFAN in the TropfishR and fishboot packages have a goodness-of-fit measure (i.e. the Rn score). We did not rely on this measure when assessing the growth curves since some of the curves with the highest Rn scores were the curves that indicated a maximum length too short or a maximum age too young when compared to prior knowledge of the species in the area. However, we report this value in the results for clarity and transparency. For an illustration of rejected curves, see Supplementary Material Figure S1.

The optimized ELEFAN function based on the genetic algorithm (ELEFAN_GA_boot; from the R package fishboot) repeatedly suggested growth patterns that were too fast and most of the rejected curves were estimated using this function. The algorithm based on the simulated annealing (ELEFAN_SA_boot) estimated growth patterns that did align with prior knowledge that the oldest oysters would be around 11 years old. Higher moving average settings (7 and 9) produced curves with poorer fits to prior expectations and most of the retained curves had a moving average setting of 5, the lowest value tested. Seven of the 36 growth curves managed to produce curves that matched

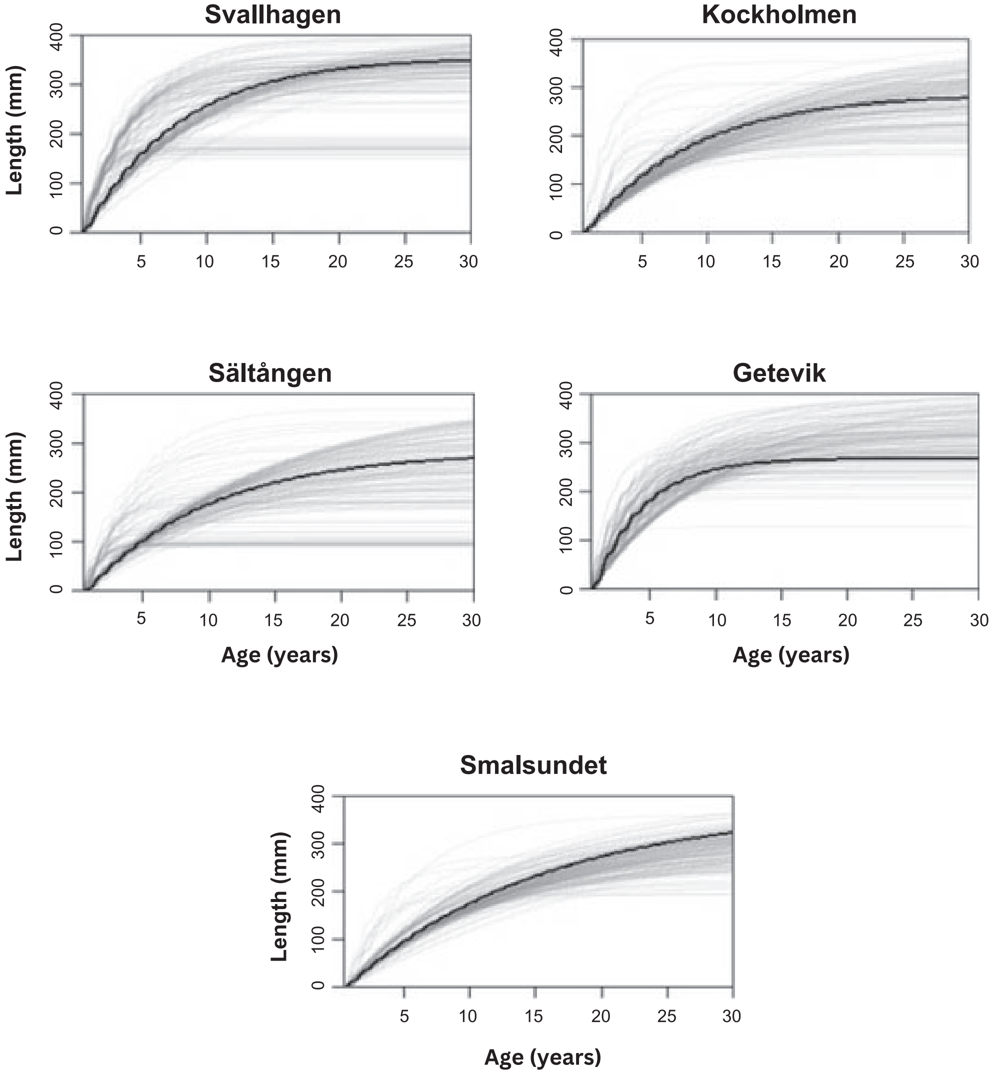

**Figure 3.** Estimated length-at-age relationships for the Pacific oyster in each of the five sites along the Swedish west coast. The thick black line represents the best estimate identified through maximum density and the grey lines are the other 199 runs of the bootstrapped ELEFAN. All curves are estimated using the simulated annealing function and a moving average setting of 5.

prior expectations and fitted the data well. For brevity and clarity, we display one curve from each location, all estimated using the simulated annealing function and a moving average setting of 5 (Fig. 3). The other two curves that performed well were the simulated annealing with a moving average of 9 at Kockholmen and the genetic algorithm with a moving average setting of 5 at Getevik.

None of the growth curves estimated for the combined site data managed to capture a reasonable growth pattern and all six curves were, therefore, excluded since they estimated that the largest oysters in the data were too young.

### *Length-at-age relationships*

Two growth patterns emerged from the seven retained curves, where Pacific oysters at Getevik and Svallhagen share a similar trajectory and individuals at Kockholmen, Sältången and Smalsundet share another (Fig. 3; Table 2). During the first year after settlement, oysters at all five sites reach sizes between 10 and 15 mm. However, at 2 years-old, the populations start to diverge and individuals at Getevik and Svallhagen continuously show faster lengthening rates compared to populations at Kockholmen, Sältången and Smalsundet (Fig. 3; Table 2). The curve for the combined sites estimated continuously larger sizes of the oysters at each age (i.e. a faster growth pattern) (Table 2), which further reflects its poor fit. The estimated size at age 11 years for all sites is close to the largest oyster measured (assumed to be 11 years-old) for each population in the sample data (Tables 1 and 2).

### *Seasonal von Bertalanffy growth function parameters*

The maximum length ($L_\infty$) of the Pacific oysters across the five sites on the Swedish west coast ranged between 266.7 and 375.3 mm, a difference of 108.6 mm (Table 2). With an estimated growth constant ($K$) of 0.27 year$^{-1}$, the growth rate was fastest at Getevik. Kockholmen, Sältången, Smalsundet and Svallhagen had relatively slower growth rates between 0.07 and 0.14 year$^{-1}$. The curve for the combined data estimated the growth rate at 0.34 year$^{-1}$, which is faster than any of the estimates for the separated five sites (Table 2). The window for the time of year that the Pacific oyster settles (*t_anchor*) in Sweden was estimated to be narrow, between 0.69 and 0.73, translating to a time of settlement at the end of September. The growth curve for the combined sites suggested a time of settle-

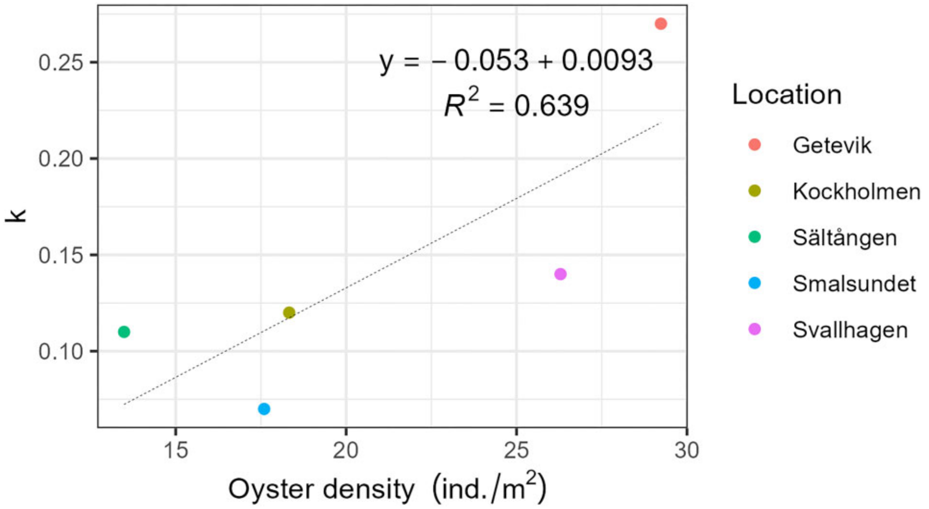

**Figure 4.** The correlation between the growth constant ($K$) from the length-at-age relationships of the Pacific oysters estimated through the ELEFAN and the density of the species (ind./$m^2$) at each of the five sample sites on the Swedish west coast ($r^2 = 0.639$, $P < 0.05$).

ment in mid-July (0.54; Table 2). The first parameter that measured the impact of season, the depth of the growth oscillation ($C$), suggested that the growth of the oysters slows down, but is not halted, during the colder months of the year (0.65 and 0.79; Table 2). The second seasonal parameter, the time of year when the growth turns positive after the winter point ($t_s$), indicated that this occurs between 1 July and late September (0.50–0.69; Table 2). All parameter values quoted are based on the simulated annealing function with a moving average setting of 5.

Finally, the estimated growth constant ($K$) was positively correlated with the median density of Pacific oysters over the sampled years, which indicates that individuals growing in dense habitats grow faster in length than those in less dense habitats (Fig. 4; $r^2 = 0.64$, $P < 0.05$).

## DISCUSSION

Here, we have estimated length-at-age relationships for five populations of wild Pacific oysters in the core area of its northernmost distribution range in Europe and demonstrated heterogeneity in growth across sites. Combining the observations from all populations did not produce a growth curve that could adequately capture the growth pattern at individual sites, and the results therefore indicate that site-specific management strategies are important to consider when developing a monitoring programme for the species' continued dispersal. Furthermore, the identified differences in growth between sites show that the analytical method used managed to capture phenotypic plasticity between the populations. In the paragraphs below, we comment on the implications of our work in terms of both methodology and the potential causal explanations for differences in growth between sites.

Two growth patterns appear among the five locations, a faster initial growth at site Getevik and Svallhagen, and a slower initial growth at Kockholmen, Sältången and Smalsundet. Consequently, this indicates that the length-at-age relationship varies among Pacific oyster sites in Sweden. At the age of 1 year, sites share similar predicted lengths of 10–15 mm; however, at age 2 years, oysters at Getevik and Svallhagen attain lengths between 60 and 75 mm, while oysters at Kockholmen, Sältången and Smalsundet only reach lengths of 35–40 mm. The pattern of longer oysters at Getevik and Svallhagen continues through the years and at age 11 years (the maximum age of the oysters in 2018); the oysters here attain lengths between 250 and 270 mm, whilst oysters at Kockholmen, Sältången and Smalsundet reach lengths between 190 and 200 mm. Moreover, the analysis indicates that individuals growing in dense habitats grow faster in length compared those in less dense habitats.

All six growth curves created to assess homogeneity between sites (using combined data from all locations) provided poor fits to the data and conflict with known properties of the populations because they suggested a maximum age of the oldest oysters that were too young (<7 years) in 2018. Furthermore, the failure of these curves to capture an appropriate growth pattern is evident when comparing the suggested length-at-age relationship of the combined data to those of the individual sites. The relationship for the combined sites suggests a faster growth pattern to those of the individual locations. While the individual sites have lengths of 10–15 mm at year one, the curve for the combined data estimates a length of 70 mm. Similarly, at age 2 years, where the growth curves for the individual sites suggest lengths between 35 and 75 mm, the combined sites predict lengths of 140 mm. This pattern continues up to the 11-year mark. This indicates that one curve cannot adequately capture the growth pattern along the whole coastline and is further evidence that there are differing growth patterns present between sites.

The continuously higher length-at-age relationships for the populations at Getevik and Svallhagen and the failure of the combined data to capture a biologically reasonable growth pattern could have two explanations. First, the differences could be due to higher bivalve densities at Getevik and Svallhagen (Fig. 4) and reflect plastic changes in shell shape that appear as heightened growth in length-frequency data. Shell growth of Pacific oysters is very plastic and is impacted by oyster density and substrate, with more elongated shells in areas with high densities or soft-bottom substrates compared to areas with lower densities or firm substrates (e.g. sand and shell hash; own observations). The substrate conditions at the surveyed sites were similar, hence, the observed higher initial asymptotic lengths ($L_\infty$) in the ELEFAN for Getevik and Svallhagen are likely a result of high oyster densities at these sites, resulting in longer shells compared to locations with lower oyster densities. Subsequently, since the ELEFAN infers age from length, the model assumes that longer oysters are older than the rounder ones, which need not necessarily be true. Future size-frequency data collection should consider measuring multiple dimensions of individual oysters (e.g. length, height and width) to better model whole-body growth. Alternatively, studies using ELEFAN should sample population levels at varying densities so that the partial effect of density can be directly estimated and accounted for. Second, previous studies that have identified heterogeneity in growth between sites have attributed these differences to environmental variables

(Askew, 1972; Gagnery *et al.*, 2003; Diederich, 2006; Harding & Mann, 2006; Cardoso *et al.*, 2007; Pogoda *et al.*, 2011; Strand *et al.*, 2012). In this study, water depth, substrate, sea temperature, salinity and exposure did not differ much between the sites. The maximum depth ranged between 105 and 148 cm, the substrates were 'walkable' sand and shell hash that became softer with depth, sea temperature and salinity showed no major shifts over the distance between the sites (Baltic Sea Physics Analysis and Forecast, 2024) and wave exposure evaluated from the SAKU data (Naturvårdsverket, 2006) was extremely sheltered or very sheltered. Lastly, food availability would not have been of general concern since the area is rather eutrophicated. Even if food availability could be a limiting factor among the high-density populations, we assume this condition would cause slower growth rates than the ones observed at the sites with lower oyster densities. Due to the similar environmental conditions across sites, the estimated faster growth patterns at Getevik and Svallhagen are most likely a result of higher oyster densities at these locations.

Looking at the length-at-age relationship of all populations at age 11 years, all estimates are similar to the largest individual measured at each site. This shows that the ELEFAN has managed to capture reasonable maximum lengths at each site for the oldest individuals. Furthermore, at 11 years-old, populations at Kockholmen, Sältången and Smalsundet indicate that the oysters are still growing towards their asymptotic lengths ($L_\infty$), suggesting that the populations on the Swedish west coast may be able to attain larger sizes than what has currently been measured. Getevik seems to be an exception, since its curve has already tapered off close to its maximum length of 266.7 mm at 11 years old. In line with the criticism by Schwamborn *et al.* (2018, 2019), the fact that the asymptotic length is still increasing at the maximum age in 2018 shows the importance of not unduly restricting the maximum lengths of the populations prior to implementing ELEFAN. If we would have relied on the size of the largest individual in each population, we would have set an upper size limit too small, and the ELEFAN would not have been allowed to investigate parameter combinations with higher maximum lengths. All populations in our study have predicted asymptotic lengths longer than the largest individual at each site.

The growth curve for Svallhagen is initially steeper than the other sites, but its estimated growth constant ($K = 0.14$ year$^{-1}$) is similar to that of Kockholmen ($K = 0.12$ year$^{-1}$) and Sältången ($K = 0.11$ year$^{-1}$). Besides the effect of density on growth, these similarities could be explained by the compensatory relationship between the asymptotic length parameter ($L_\infty$) and the growth constant ($K$). A higher asymptotic length is often associated with a lower growth constant. Conversely, a lower maximum length is often coupled with a higher growth constant. The maximum length at Svallhagen was estimated as 354.0 mm and the predictions for Kockholmen and Sältången were 284.2 and 281.9 mm, respectively. Therefore, oysters at Kockholmen and Sältången are expected to reach their asymptotic length sooner than the individuals at Svallhagen, which has resulted in similar growth constant values for the three sites.

All five populations show a noticeable impact of season, which aligns with previous studies, which have reported changes in Pacific oyster growth related to the time of year (e.g. Cardoso *et al.*, 2007; Góngora-Gómez *et al.*, 2017). The parameter associated with the amplitude of the decrease in growth at the depth of the growth oscillation ($C$) was estimated between 0.65 and 0.79 and indicates that the growth of the Pacific oysters is reduced, but not stopped, during the colder months in northern Europe. The second seasonal parameter, the time of the year that the growth turns positive after the winter point ($t_s$), indicated that this happens between 1 July and late September, which is relatively late in the year.

The curves generally provided an adequate fit to the data and prior knowledge of the species. However, the parameter for the time of year that the oysters settle on the Swedish west coast (*t_anchor*) was estimated for late September for all five sites. Previous studies have found that Pacific oysters in Sweden often settle in high densities in July and August (Dunér Holthuis *et al.*, 2014). However, the spawning time of the oysters (Mann, 1979) and larval development time to settlement (Helm & Bourne, 2004) are also known to vary with abiotic conditions (i.e. temperature). In accordance, the spawning time of Pacific oysters has been observed to vary between years in Sweden, with earlier spawning, two spawning events (beginning of July and end of August) occurring during extremely warm years (as in Dunér Holthuis *et al.*, 2014), and later spawning (end of August) under more normal conditions (Lewis *et al.*, 2023). This is well in accordance with the model predictions given the expected development time of the oyster larvae of 16–20 days (Helm & Bourne, 2004). However, factors impacting population dynamics may also affect model predictions. In the current data, two occasions with mass mortalities were observed; one during the winter 2009/2010, which was a very harsh winter that killed many oysters (Strand *et al.*, 2012), and one during summer/autumn 2014 where the first oyster herpes virus outbreak was observed and documented (Mortensen *et al.*, 2016), leaving populations of smaller sizes for the sampling the following year(s).

### *Success of TropfishR and fishboot*

Using **TropfishR** (Mildenberger *et al.*, 2017a, b; Mildenberger, 2017c) and **fishboot** (Schwamborn *et al.*, 2018), we identified at least one growth curve for each site that provided a biologically reasonable growth pattern. Six out of the seven accepted curves were estimated using the bootstrap function based on the simulated annealing (**ELEFAN_SA_boot**). The function based on the genetic algorithm (**ELEFAN_GA_boot**) continuously suggested growth patterns that were not plausible. However, other studies have found the GA function to provide the best estimates of growth (Taylor & Mildenberger, 2017), which suggests that the choice of the ELEFAN function could depend on the study species. Additionally, contrary to Taylor & Mildenberger (2017), higher moving average settings in our analysis did not result in growth curves with better fits, since those settings suggested the oysters were much younger than we know them to be. Most of the accepted curves (six out of seven) in the current study had a moving average setting of 5, the lowest value tested.

In their demonstration of the **TropfishR** package, Taylor & Mildenberger (2017) concluded that the two optimization functions (**ELEFAN_SA** and **ELEFAN_GA**) did manage to produce curves with high Rn scores. However, they also concluded that there is no guarantee that 'true' seasonally oscillating von Bertalanffy growth parameter combinations will result in the highest Rn score. We suggest that an important step in this methodology lies in the visual inspection of how fitted curves align with observations and prior expectations. Even if a growth pattern seems reasonable and the curve obtains a high goodness-of-fit score, it does not necessarily mean that the fit of the curve to the data is good. A critical aspect of the analysis is, therefore, to evaluate how well the growth curves fit the reconstructed length-frequency data and how well they match prior information about the growth of the analysed species.

## CONCLUSION

We have predicted length-at-age relationships for the Pacific oyster in Sweden that can be used both for future stock assessments of this species in northern Europe, including estimations of recruitment patterns, mortality and sustainable harvesting yields, and for designing mitigation efforts. Through the length-at-age relationships, we found that the oysters grow at different rates at different locations. Since the environmental conditions did not differ much across the sites in this study, we assume that the different growth patterns are mostly linked to bivalve density. We conclude, therefore, that site-specific management may be important, where high-density sites should be prioritized to reduce the ecological impact and reproductive standing stock of the oysters. Because of potential plasticity in growth form, we also suggest that future studies of Pacific oyster growth should collect measurements of additional dimensions of the oysters, such as width and height to facilitate more meaningful contrasts of growth and plasticity across populations. The use of the R packages TropfishR and fishboot was successful in estimating growth patterns for the wild Pacific oyster in northern Europe. However, since 29 out of 36 growth curves were excluded due to suggesting non-reasonable growth patterns, an important aspect of using these methods lies in the evaluation of how well the curve fits the reconstructed length-frequency data.

## SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

## ACKNOWLEDGEMENTS

The authors thank assistants, students and collaborators who contributed to the field work. We also thank the editor and two anonymous reviewers for comments on earlier versions of the manuscript.

## FUNDING

Å.S. received funding from Formas (Dnr 2011-1132), the Swedish Agency for Marine and Water Management through Havsmiljöanslaget Dnr. 309-1719-09 and Wåhlström's Foundation. A.T.L. acknowledges funding from the Royal Swedish Academy of Sciences, Helge Ax: son Johnsson Foundation, Wåhlström's Foundation, and the Nordic Council of Ministers (through the project 'Harvestable Pacific oysters. Collecting background data and estimating the standing stock, for a better management and the development of a commercial harvest of Pacific oysters, *Crassostrea gigas*').

## CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

## DATA AVAILABILITY

Data are available on request to the corresponding author.

## REFERENCES

ASKEW, C.G. 1972. The growth of oysters *Ostrea edulis* and *Crassostrea gigas* in Emsworth harbour. *Aquaculture*, **1**: 237–259.

BALTIC SEA PHYSICS ANALYSIS AND FORECAST. E.U. 2024. Copernicus Marine Service Information (CMEMS). Marine Data Store (MDS). DOI: 10.48670/moi-00010 (21 November 2024, date last accessed).

BRETT, J.R. 1979. Environmental factors and growth. *Fish Physiology*, **8**: 599–675.

CARDOSO, J., LANGLET, D., LOFF, J., MARTINS, A., WITTE, J., SANTOS, P. & VAN DER VEER, H. 2007. Spatial variability in growth and reproduction of the pacific oyster *Crassostrea gigas* (Thunberg, 1793) along the west European coast. *Journal of Sea Research*, **57**: 303–315.

DIEDERICH, S. 2006. High survival and growth rates of introduced Pacific oysters may cause restrictions on habitat use by native mussels in the Wadden Sea. *Journal of Experimental Marine Biology and Ecology*, **328**: 211–227.

DOLMER, P., HOLM, M.W., STRAND, Å., LINDEGARTH, S., BODVIN, T., NORLING, P. & MORTENSEN, S. 2014. The invasive Pacific oyster, *crassostrea gigas*, in Scandinavian coastal waters: a risk assessment on the impact in different habitats and climate conditions. *Fisken of Havet, Institute of Marine Research*, **2**: 1–67.

DOWLING, N.A., DICHMONT, C.M., HADDON, M., SMITH, D.C., SMITH, A.D.M. & SAINSBURY, K. 2015. Empirical harvest strategies for data-poor fisheries: a review of the literature. *Fisheries Research*, **171**: 141–153.

DUNÉR HOLTHUIS, T., THORNGREN MATTSSON, L., LINDEGARTH, M. & LINDEGARTH, S. 2014. *Utveckling av Metodik för Insamling av Ostronyngel—Ett Småskaligt System för Ostronproduktion i Bohuslän. Rapport No. 3*, från Vattenbrukscentrum Väst, Göteborgs Universitet.

EKELUND, U., HÅKANSSON, M. & HAAMER, J. 1977. En undersökning om förutsättningarna för ostronodling vid svenska västkusten. *Chalmers Tekniska Högskola och Göteborgs Universitet*, **83**: 1–35. [In Swedish ].

GAGNERY, A., CHABIRAND, J.-M., LAGARDE, F., LE GALL, P., OHEIX, J., BACHER, C. & BUESTEL, D. 2003. Growth model of the Pacific oyster, *crassostrea gigas*, cultured in Thau Lagoon (Mediterranee, France). *Aquaculture*, **251**: 267–290.Aquaculture, volume 251, Issues 1-4, Pages 267-290.

GAYANILO, F.C. & PAULY, D. (eds) 1997. *FAO-ICLARM stock assessment tools: reference manual.* Food and Agriculture Organization of the United Nations, Rome.

GAYANILO, F.C., SPARRE, P. & PAULY, D. 1996. FAO-ICLARM Stock Assessment Tools II (FiSAT II). Revised version. User's guide. *FAO Computerized Information Series (Fisheries)*, **8**: 1–168.

GENERAL FISHERIES COMMISSION FOR THE MEDITERRANEAN (GFCM). 2022. Report of the eighth meeting of the Subregional Group on Stock Assessment in the Black Sea (SGSABS). https://www.fao.org/gfcm/technical-meetings/detail/en/c/1609439/. (21 November 2024, date last accessed).

GÓNGORA-GÓMEZ, A.M., ARAGÓN-NORIEGA, E., DOMÍNGUEZ-OROZCO, A.L. & VILLANUEVA-FONESECA, B.P. 2017. Modeling the individual growth of the Pacific oyster *crassostrea gigas* cultivated in the Gulf of California using the von Bertalanffy model. *Revista de Biologia Marina y Oceanografia*, **52**: 181–185.

GOSLING, E. 2007. *Bivalve molluscs.* Fishing News Books, Oxford.

HARDING, J.M. & MANN, R. 2006. Age and growth of wild Suminoe (*Crassostrea ariakensis*, Fugita 1913) and Pacific oysters (*C. gigas*, Thunberg 1793) oysters from Laizhou Bay, China. *Journal of Shellfish Research*, **25**: 73–82.

HEINO, M., DIECKMANN, U. & GODØ, O.R. 2002. Estimating reaction norms for age and size at maturation with reconstructed immature size distributions: a new technique illustrated by application to Northeast Arctic cod. *ICES Journal of Marine Science*, **59**: 562–575.

HELM, M.M. & BOURNE, N. 2004. In: *Hatchery culture of bivalves—a practical manual*, (A. Lovatellied.). FAO Fisheries Department, Rome.

KRITZER, J.P. & DAVIES, C.R. 2005. Demographic variation within spatially structured reef fish populations: when are larger-bodied subpopulations more important? *Ecological Modelling*, **182**: 49–65.

LAUGEN, A., HOLLANDER, J., OBST, M. & STRAND, Å. 2015. The Pacific oyster (*Crassostrea gigas*) invasion in Scandinavian coastal waters in a changing climate: impact on local ecosystem services. In: *Biological invasions in changing ecosystems*. (J. Canning-Clode, ed.), pp. 230–252. De Gruyter Open, Poland.

LEWIS, L., WRANGE, A.-L., FABIOUX, C., SÜHNEL, S. & STRAND, Å. 2023. *Validation of a temperature-maturation model for M. gigas in Swedish waters: implications for cultivation and management*. AquaNor, Trondheim.

LORENZEN, K. 2016. Toward a new paradigm for growth modeling in fisheries stock assessments: embracing plasticity and its consequences. *Fisheries Research*, **180**: 4–22.

MANN, R. 1979. Some biochemical and physiological aspects of growth and gametogenesis in *Crassostrea gigas* and *Ostrea edulis* grown at sustained elevated temperatures. *Journal of the Marine Biological Association of the United Kingdom*, **59**: 95–110.

METHOT, R.D. & WETZEL, C.R. 2013. Stock synthesis: a biological and statistical framework for fish stock assessment and fishery management. *Fisheries Research*, **142**: 86–99.

MILDENBERGER, T.K. 2017. Single-species fish stock assessment with TropFishR. The Comprehensive R Archive Network. https://cran.r-project.org/web/packages/TropFishR/vignettes/tutorial.html. (21 November 2024, date last accessed).

MILDENBERGER, T.K., TAYLOR, M. & WOLFF, M. 2017a. TropFishR: an R package for fisheries analysis with length-frequency data. *Methods in Ecology and Evolution*, **8**: 1520–1527.

MILDENBERGER, T.K., TAYLOR, M.H. & WOLFF, M. 2017b. TropFishR: tropical fisheries analysis with R (version 1.1.3). https://github.com/tokami/TropFishR. (21 November 2024, date last accessed).

MORTENSEN, S., DOLMER, P., STRAND, Å., NAUSTVOLL, L.-J. & LAUGEN, A. 2019. *Policy brief: the Pacific oyster—a new Nordic food resource and a basis for tourism*. Nordic Council of Ministers, Copenhagen.

MORTENSEN, S., LAUGEN, A.T., STRAND, Å., DOLMER, P., NAUSTVOLL, L.-J., JELMERT, A., ALBRETSEN, J., BROSTRÖM, G., GUSTAFSSON, M., DURKIN, A., KHOGYANE, S.E., PARTOFT, H. & BØGWALD, M. 2022. Stillehavsøsters i Norden. Datainnsamling og bestandsvurderinger som grunnlag for forvaltning og høsting av nordiske bestander av stillehavsøsters *Crassostrea gigas*. *Nordisk Ministerråd*, **504**: 1–61. [ In Norwegian].

MORTENSEN, S., STRAND, Å., BODVIN, T., ALFJORDEN, A., SKÅR, C.K., JELMERT, A., ASPÁN, A., SÆLEMYR, L. & NAUSTVOLL, L.-J. 2016. Summer mortalities and detection of ostreid herpesvirus microvariant in pacific oyster *crassostrea gigas* in Sweden and Norway. *Diseases in Aquatic Organisms*, **117**: 171–176.

NATURVÅRDSVERKET. 2006. SAKU—Sammanställning och analys av kustnära undervattenmiljö. *Naturv å rdsverket*, rapport 5591. ISBN 91-620-5591-7. [ In Swedish].

NEHLS, G., DIEDERICH, S., THIELTGES, D. & STRASSER, M. 2006. Wadden Sea mussel beds invaded by oysters and slipper limpets: competition or climate control? *Helgoland Marine Research*, **60**: 135–143.

NEHRING, S. 2011. NOBANIS—Invasive alien species fact sheet—*Crassostrea gigas*. From: online Database of the European Network on Invasive Alien Species—NOBANIS. www.nobanis.org. (29 June 2023, date last accessed).

NUSSEY, D.H., WILSON, A.J. & BROMMER, J.E. 2007. The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of Evolutionary Biology*, **20**: 831–844.

PAULY, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil*, **39**: 175–192.

PAULY, D. 1987. A review of the ELEFAN system for analysis of length-frequency data in fish and aquatic invertebrates. In: *Length-based Methods in Fisheries Research* (D. Pauly & G.R. Morgan, eds.), pp. 7–34. ICLARM Conference Proceedings 13. International Center for Living Aquatic Resources Management, Manila, Philippines, and Kuwait Institute for Scientific Research, Safat.

PAULY, D. & DAVID, N. 1981. ELEFAN 1, a BASIC program for the objective extraction of growth parameters from length-frequency data. *Berichte Der Deutschen Wissenschaftlichen Kommissuib Fu¨r Meeresforschung*, **28**: 205–211.

PAULY, D. & GASCHÜTZ, G. 1979. *A Simple Method for Fitting Oscillating Length Growth Data, with a Program for Pocket Calculators*. Paper presented at the Council Meeting of the International Council for the Exploration of the Sea. CM 1979/G24, Demersal Fish Ctte, pp. 1–26.

PIGLIUCCI, M., MURREN, C.J. & SCHLICHTING, C.D. 2006. Phenotypic plasticity and evolution by genetic assimilation. *Journal of Experimental Biology*, **209**: 2362–2367.

POGODA, B., BUCK, B.H. & HAGEN, W. 2011. Growth performance and condition of oysters (*Crassostrea gigas* and *Ostrea edulis*)—farmed in an offshore environment (North Sea, Germany). *Aquaculture*, **319**: 484–492.

R CORE TEAM. 2024. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/. (21 November 2024, date last accessed).

SALVI, D. & MARIOTTINI, P. 2017. Molecular taxonomy in 2D: a novel ITS2 rRNA sequence-structure approach guides the description of the oysters' subfamily saccostreinae and the genus *Magallana* (Bivalvia: ostreidae). *Zoological Journal of the Linnean Society*, **179**: 263–276.

SALVI, D. & MARIOTTINI, P. 2021. Revision shock in Pacific oysters taxonomy: the genus *Magallana* (formerly *Crassostrea* in part) is well founded and necessary. *Zoological Journal of the Linnean Society*, **192**: 43–58.

SCHWAMBORN, R. 2018. How reliable are the Powell–Wetherall plot method and the maximum-length approach? Implications for length-based studies of growth and mortality. *Reviews in Fish Biology and Fisheries*, **28**: 587–605.

SCHWAMBORN, R., MILDENBERGER, T. & TAYLOR, M. 2019. Assessing sources of uncertainty in length-based estimates of body growth in populations of fishes and macroinvertebrates with bootstrapped ELEFAN. *Ecological Modelling*, **393**: 37–51.

SCHWAMBORN, R., MILDENBERGER, T.K. & TAYLOR, M.H. 2018. *Fishboot: bootstrap-based methods for the study of fish stocks and aquatic populations*. R package version 0.1.1. https://www.R-project.org/. (21 November 2024, date last accessed).

SOMERS, I.F. 1988. On a seasonally oscillating growth function. *Fishbyte*, **6**: 8–11.

SPARRE, P. & VENEMA, S.C. 1998. *Introduction to Tropical Fish Stock Assessment—Part 1: Manual*. Food and Agriculture Organization of the United Nations (FAO). Fisheries Technical Paper. No. 306.1, Rev. 2. FAO, Rome.

STEARNS, S.C. & KOELLA, J.C. 1986. The evolution of phenotypic plasticity in life history traits: predictions of reaction norms for age and size at maturity. *International Journal of Organic Evolution*, **40**: 893–913.

STRAND, Å., BLANDA, E., BODVIN, T., DAVIS, J.K., JENSEN, L.F., HOLM-HANSEN, T.H., JELMERT, A., LINDEGARTH, S., MORTENSEN, S., MOY, F.E., NIELSEN, P., NORLING, P., NYBERG, C., CHRISTENSEN, H.T., VISMANN, B., WEJLEMANN HOLM, M., WINDING HANSEN, B. & DOLMER, P. 2012. Impact of an icy winter on the Pacific oyster (*Crassostrea gigas* Thunberg, 1793) populations in Scandinavia. *Aquatic Invasions*, **7**: 433–440.

STRAND, Å. & LINDEGARTH, S. 2014. *Japanska Ostron i Svenska Vatten—en Främmande Art Som Är Här För Att Stanna. Rapport No. Vattenbrukscentrum Väst, Göteborgs universitet*. Responstryck, Bosås, Sweden. [ In Swedish].

TAYLOR, M.H. & MILDENBERGER, T.K. 2017. Extending electronic length frequency analysis in R. *Fisheries Management and Ecology*, **24**: 330–338.

TROOST, K., STAMHUIS, E., VAN DUREN, L. & WOLFF, W. 2009. Feeding current characteristics of three morphologically different bivalve suspension feeders, *Crassostrea gigas*, *Mytilus edulis* and *Cerastoderma edule*, in relation to food competition. *Marine Biology*, **156**: 355–372.

VON BERTALANFFY, L. 1938. A quantitative theory of organic growth (inquiries on growth laws. II). *Human Biology*, **10**: 181–213.

WOLFF, M. 1989. A proposed method for standardization of the selection of class intervals for length frequency analysis. *Fishbyte*, **7**: 5.

WRANGE, A., VALERO, J., HARKESTAD, L., STRAND, Ø., LINDEGARTH, S., CHRISTENSEN, H., DOLMER, P., KRISTENSEN, P. & MORTENSEN, S. 2010. Massive settlements of the Pacific oyster, *Crassostrea gigas*, in Scandinavia. *Biological Invasions*, **12**: 1145–1152.