

Spatial variation in growth rate of early juvenile European plaice *Pleuronectes platessa*

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ABSTRACT: Patterns and causes of spatial variation in RNA-predicted growth rates in mid-August were examined in young-of-the-year European plaice *Pleuronectes platessa* ('YOY plaice') at 22 beaches along a 300 km stretch of coastline in west Scotland in 3 consecutive years. According to restricted maximum likelihood models, growth rates varied among beaches (25 km scale), but these spatial patterns were not consistent across years. We found no evidence for spatial variation in growth at the scale of subregions (50 km) or regions (100 km). Growth rate was positively correlated with total length, both within and among beaches and years. In general, YOY plaice in mid-August grew more slowly than estimated ad libitum laboratory rates. Average growth rates by beach and year were inversely related to intraspecific competitor densities, but not interspecific competitor densities (brown shrimp *Crangon crangon*) or 2 environmental productivity metrics (nearshore chlorophyll *a* concentration and lugworm *Arenicola marina* cast density). Physical beach characteristics also explained a significant source of spatial growth variation, with fish growing faster at beaches with larger tidal range and wave fetch. Therefore, the hypothesis of sub-maximum growth due to intraspecific competition (density-dependent growth) was supported, but additional, previously unexplored processes related to physical beach characteristics appear to have important influences on the spatial growth dynamics of YOY plaice.

KEY WORDS: Density dependence · 0-group flatfish · Recruitment · Benthic food web · Sandy beaches · Production · RNA:DNA ratio · Scottish sea lochs

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INTRODUCTION

Spatial and temporal patterns of variability are the fundamental motivation for hypotheses and theories to explain the function of ecological systems (Underwood et al. 2000). Knowledge of such patterns facilitates observational studies and guides the design of manipulative experiments to understand these functions (Hurlbert 1984, Eberhardt & Thomas 1991). In particular, understanding patterns of variation allows confounding influences of processes operating at different spatial and temporal scales to be separated and efforts to be focused on the domains of scale over

which variation is largest (Hurlbert 1984, Wiens 1989, Levin 1992). Patterns of variation in species abundance and community structure have received considerable attention in the ecological literature (Thrush 1991, Morrissey et al. 1992), but there is less information regarding other important ecological variables such as growth and mortality.

Growth and mortality during juvenile stages are thought to influence the population dynamics of fishes and other high-fecundity marine species (Sissenwine 1984, Houde 1987, Bradford & Cabana 1997). There can be large mismatches between spatial scales at which these critical processes are controlled and

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scales at which their population-level consequences are manifested (Forrester et al. 2008). Many marine fishes are mobile, undertake considerable feeding and spawning migrations, and have highly dispersive larval stages (Pittman & McAlpine 2003), and therefore constitute relatively open populations that rely on spatially-extensive inshore areas as juveniles (Hixon et al. 2002, Watts et al. 2010). In contrast, individual juveniles often have relatively small home ranges, restricted to a tiny fraction of the total juvenile habitat (Pittman & McAlpine 2003), for example a short stretch of beach (Burrows et al. 2004) or a single coral colony (Sale 1971). Furthermore, juvenile fish habitats are often characterized by small-scale heterogeneity in environmental conditions (Stierhoff et al. 2009). Therefore, causes of juvenile growth and mortality are fine-grained, local processes, but population- and larger-scale consequences are the outcome of large numbers of these processes occurring over extensive networks of nurseries. The functional role of juvenile habitats for marine fishes must be addressed within a fine-grained and spatially-extensive framework. This framework must also recognize the scale-dependence of spatial growth variation in order to identify the important domains of scale over which controlling processes operate.

A fine-grained, spatially-extensive and spatial scale-dependent understanding of variation in growth of young-of-the-year European plaice *Pleuronectes platessa* ('YOY plaice'), for example, is lacking, despite the long history of research into causes of growth variation in this species. Plaice is a commercially important flatfish species distributed across the northeast Atlantic, from Greenland and Norway south to Morocco, and in the western Mediterranean (Nielsen 1986). YOY plaice inhabit shallow (ca. 1 to 2 m), sandy, moderately exposed areas during the summer (Gibson 1999). Considerable debate has focused on whether growth rates in these environments are maximum and controlled by temperature alone (the 'maximum growth/optimal food condition' hypothesis, sensu Karakiri et al. 1991, van der Veer & Witte 1993) or whether there is density-dependent or density-independent food limitation. Recent evidence suggests that growth is close to maximum after settlement, but becomes limited and may even cease later in the summer (Jager et al. 1995, van der Veer et al. 2010, Ciotti et al. in press). Although declines in growth rate during the summer are common to most nurseries studied, the slope and intercept is spatially variable (Ciotti et al. 2010, in press).

Causes of growth limitation of YOY plaice in late summer remain uncertain. While food limitation is

likely, it is unclear whether the density of prey and/or intraspecific competition are ultimately responsible (Teal et al. 2008, van der Veer et al. 2010). Furthermore, previous studies have highlighted the potential importance of interspecific competition in plaice nursery areas (Evans 1983, Pihl 1985). Some authors have suggested that interspecific competition may be responsible for the widely observed growth limitation in late summer (Jager et al. 1995, Teal et al. 2008, van der Veer et al. 2010), but only 2 studies have tested this possibility directly (Freitas et al. 2010, Ciotti et al. in press). Therefore, combined influences of environmental (prey) productivity and the density of intra- and interspecific competitors on growth rates in late summer require testing.

There is also a need to explore new variables that could generate hypotheses to explain growth variation in late summer. Exploratory analyses should start with variables that have broad, overarching influences on environmental conditions in plaice nursery habitats, such as wave fetch, tidal range, and openness. Wave fetch is a principal determinant of abiotic (particle size, beach morphology, temperature, water movement, physical disturbance) and biotic (structure and function of competitor, predator, and prey communities) conditions in shallow, sandy habitats (McLachlan & Brown 2006), including plaice nursery areas (McIntyre & Eleftheriou 1968, McIntyre et al. 1970), and is thought to influence habitat use (Steele et al. 1970, Berghahn 1987) and food intake (Lockwood 1980, 1984) in YOY plaice. Tidal range influences beach morphology as well as the quality and quantity of intertidal habitat occupied by YOY plaice at high tide (McLachlan & Brown 2006). Openness describes the area of water connected to a site within a given radius and might influence key ecological processes, such as larval transport, circulation, or terrestrial influences in coastal areas (Burrows et al. 2010). Wave fetch, tidal range, and openness are key variables defining environmental conditions of plaice nursery habitats, and their association with YOY plaice growth should be explored.

Detailed measurements of broad-scale, spatial variation in short-term growth rate of YOY plaice in late summer combined with measurements of environmental variability could now yield important insights into causes of growth limitation during this period. Although studies have been conducted in diverse locations throughout Europe, most have focused on small (<10 km²), discrete areas of nursery habitat, and provide little information about growth variation in a broader spatial context (Ciotti 2012). Studies that have examined growth variation at

larger scales (Poxton et al. 1983, van der Veer & Witte 1993, Haynes et al. 2012) have used integrated growth metrics, such as size-frequency progression, that are not sensitive to short-term or local causes of growth variation. Recently, high-throughput biochemical tools have been developed that can estimate short-term individual growth rate in YOY plaice (Ciotti et al. 2010). These tools now provide opportunities to test existing hypotheses and explore new variables to explain growth variation in YOY plaice within an appropriate spatial framework that recognizes the short-term causes, the spatial scale-dependence of controlling processes, and the broad-scale population implications.

In this study, variation in RNA-predicted growth rates of individual YOY plaice was characterized at 22 nursery beaches on the west coast of Scotland in August, for 3 consecutive years. We compared growth variation at 3 nested spatial scales ranging from beaches (25 km scale) to regions (100 km scale; 'unconditional model' comparisons). We assessed the frequency and magnitude of growth limitation at these scales and tested the hypothesis that growth in late summer is maximum and limited by temperature alone against hypotheses of food limitation due to intra- and interspecific competitor densities and environmental productivity ('hypothetical model' comparisons). Finally, in order to generate new hypotheses to explain growth variation in late summer, we explored relationships between growth rate and 3 physical variables with overarching influences on abiotic and biotic conditions in YOY plaice nursery habitats: wave fetch, openness, and tidal range ('exploratory model' comparisons).

MATERIALS AND METHODS

Data collection

Field sampling

Sampling was conducted at 22 beaches spanning a 300 km stretch of the west coast of Scotland (Fig. 1). To compare growth variation among spatial scales, sampling locations were selected according to a spatially nested design, with 1 to 3 study beaches (25 km scale) nested within 1 or 2 subregions (50 km scale), nested within 5 regions (100 km scale; Fig. 1). All beaches were sampled once in August from 2005 to 2007. In a given year, sampling was completed within a 10 d period. Sampling dates (17 to 26 August 2005, 7 to 15 August 2006, 10 to 19 August 2007) and

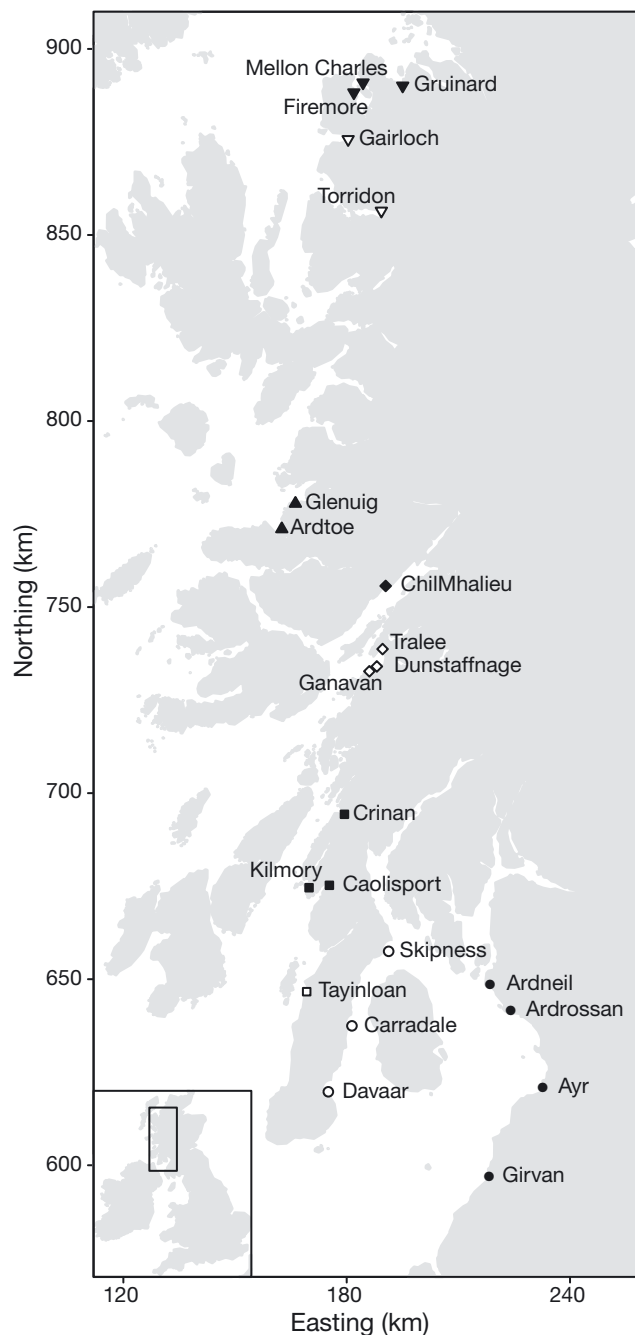


Fig. 1. Beaches sampled in Scotland in mid-August 2005 to 2007 to characterize broad-scale spatial growth variation in young-of-the-year European plaice *Pleuronectes platessa*. Beaches are mapped in the British National Grid coordinate system (OSGB36). Abscissa and ordinate axes represent the distance east and north, respectively, from an origin at 49° 46' N, 7° 33' W. Symbol shapes represent regions (▼ = NW Scotland, ▲ = Moidart, ◆ = Lorn, ■ = Kintyre, ● = Clyde Sea). Open and solid symbols represent different sub-regions nested within regions. Tralee and Firemore are also known as Ardmucknish Bay and Loch Ewe, respectively, in the published literature. The inset shows map location within the British Isles

the sampling order of beaches varied among years, as dictated by tidal and logistical constraints. At each beach, the same fixed station was located with GPS (Garmin 72, accuracy <15 m) and sampled within 2 h of low tide.

On each sampling occasion, replicate ($n = 2$ to 8) 1.5 m beam trawl tows (6 mm mesh, fitted with 3 tickler chains and a cod-end liner of 3 mm mesh) were hand pulled parallel to the shore at 0.5 m depth. Trawl distances were measured with a GPS attached to the trawl frame (average = 132 m, range = 38 to 380 m). Fish and macroinvertebrate catches were identified and counted. Bottom temperatures at 0.5 m depth ($T_b \pm 0.1^\circ\text{C}$) were measured with bulb and digital thermometers. To assess intertidal benthic productivity, casts of the lugworm *Arenicola marina* (L.), a common and easily measurable polychaete considered to be an index of feeding conditions for YOY plaice (van der Veer & Witte 1993), were counted at mean low water neap and at mean tide level either in 10 to 20 random 1 m² quadrats or in 1 m wide by 100 m long strips (where casts were rare). The mean of \log_{10} *A. marina* cast densities across all quadrats from both tide levels was calculated for each beach and year (P_i , $\log_{10}[\text{casts m}^{-2}]$).

Densities of YOY plaice (C_c , $\log_{10}[\text{ind. m}^{-2}]$) and brown shrimp *Crangon crangon* (L.) (C_h , $\log_{10}[\text{ind. m}^{-2}]$) were considered indices of intra- and interspecific competition, respectively. *C. crangon* are predators of small (≤ 30 mm) post-larval plaice (van der Veer & Bergman 1987, Gibson et al. 1995), but there can be considerable diet overlap between these 2 species later in the summer (Evans 1983). Densities were calculated by dividing total catch by total trawl area (= 1.5 m \times trawl distance in m) for each beach and year. YOY plaice and *C. crangon* densities were \log_{10} transformed to improve normality. Densities were not corrected for trawl efficiency. Estimates of the efficiency of small beam trawls at catching YOY plaice on sandy substrates range from 25 to 100% (Edwards & Steele 1968, Kuipers 1975, Rogers & Lockwood 1989).

All YOY plaice caught were either photographed or anaesthetized in benzocaine and preserved in 10% formalin. Fish total lengths were measured directly (preserved samples) or from photographs. Correction for shrinkage due to formalin preservation was not considered necessary (Lockwood 1973, Lockwood & Daly 1975) and was not applied. A sub-sample of 10 to 25 YOY plaice was selected haphazardly, flash-frozen immediately after capture, and stored below -70°C for subsequent nucleic acid measurement. No samples were available from Dun-

staffnage in 2005 or 2006. Sample sizes were low at ChilMhalieu in 2005 ($n = 4$) and 2007 ($n = 8$) and at Crinan in 2005 ($n = 9$).

Growth measurement

RNA and DNA concentrations were determined in 1 ca. 0.010 g sub-sample of white muscle tissue dissected from the epaxial eyed side of each fish. Dissections were performed on dry ice to minimize thawing of sub-samples. Nucleic acids in sub-samples were measured using a 1-dye, 2-enzyme fluorometric assay closely following the protocol of Caldarone et al. (2001), with minor modifications to vortexing, sonication, incubation times, and to the concentrations and volumes of nucleases, as detailed by Ciotti et al. (2010). The mean \pm SD ratio of DNA to RNA standard curve slopes across all samples was 2.25 ± 0.0736 .

Instantaneous growth rate for individual fish was estimated according to an RNA-based growth index (Ciotti et al. 2010). This index estimates the daily increment in \ln mass (G , d^{-1}) from measurements of white muscle RNA and DNA concentration, water temperature at the time of capture, and fresh body mass. Water temperatures used were those measured during sampling, as described above. Fresh body mass (M_{fresh}) was derived from frozen body mass (M_{frozen} ; measured during dissection) as $M_{\text{fresh}} = (1.0060 \times M_{\text{frozen}}) + 0.011461$. This correction was obtained using reduced major-axis regression (Pearson's $r = 0.999$) between M_{fresh} and M_{frozen} in laboratory-held fish ($n = 419$, range in $M_{\text{frozen}} = 0.46$ to 11.54 g).

All available YOY plaice samples were included in the growth analyses, regardless of size. Approximately 6% of these samples (range in $M_{\text{fresh}} = 0.29$ to 13.76 g) were outside the size range of fish used to develop the RNA-based growth index (range in $M_{\text{fresh}} = 0.44$ to 6.70 g).

Mass measurements potentially biased growth predictions in 2 ways. First, unlike fish used to develop the RNA-based growth index, masses of field fish were not corrected for gut contents. Second, the RNA-based growth index was developed using mass measured 10 d prior to sacrifice, but this information was unavailable for field fish. Trials with laboratory-held fish suggested that these inaccuracies in mass measurements would only produce small differences in predicted growth rates, and tended to overestimate the rate of positive or negative growth by ca. 5%.

Satellite data

Average sea surface temperature and chlorophyll *a* (chl *a*) concentration in summer (June to August) for each year and beach were obtained from satellite images. Images were supplied by the NERC Earth Observation Data Acquisition and Analysis Service (www.neodaas.ac.uk) as level 3 monthly composites (medians for each month and year) with ca. 1 km spatial resolution. Temperature images were combined sea and atmosphere sea surface temperatures measured with the Advanced Very High Resolution Radiometer. Chl *a* images were in-water concentrations calculated with the OC5 algorithm (Gohin et al. 2002), measured with the aqua-MODIS sensor and obtained through the US National Aeronautics and Space Administration.

Pixel locations were projected onto the British National Grid coordinate system (OSGB36) using the definition from the PROJ.4 cartographic projections library implemented in the proj4 package (Urbanek 2011) in R (R Development Core Team 2011). Coverage was calculated for each pixel as the proportion of images containing data, for the months (March to August) and years (2005 to 2007) of primary interest. For example, coverage of a pixel containing data in March 2005 and July 2007 images would be 0.11 (2 images with data out of 18 total images). The 30 pixels closest to each beach that met a minimum coverage requirement (a 'coverage cutoff') were considered to represent local sea surface temperature or chl *a* conditions. Sea surface temperature and \log_{10} chl *a* concentrations were spatially averaged (mean) in each image across this set of 30 representative pixels. With no or low coverage cutoff, spatial averages for many beaches and images would have been based on just a few pixels or would have been missing entirely. However, increasing the coverage cutoff produced averages based on pixels farther from sampling stations because higher coverage pixels were generally farther offshore. Coverage cutoffs of 0.7 (sea surface temperature) and 0.8 (chl *a* concentration) were found to maximize the data availability, while ensuring that neighboring pixels remained, on average, within ca. 10 km of their corresponding sampling site. Distances between pixels were determined by linear interpolation such that sea distances between neighboring pixels were potentially large if separated by a peninsula or narrow headland. Therefore, maps were drawn and examined to confirm that the 30 representative pixels were located in waters adjacent to each beach. Summer sea surface temperature (T_s , °C) and \log_{10} chl *a* concentration (P_p ,

$\log_{10}[\text{mg m}^{-3}]$) for each beach and year were calculated as means of spatial means for June, July, and August images.

Physical beach characteristics

Wave fetch was estimated digitally from a ca. 200 m resolution coastal grid for the UK and near continent, produced from the Global Self-consistent, Hierarchical, High-resolution Shoreline Database (GSHHS) and projected onto the British National Grid coordinate system. Wave fetch was defined as the distance to closest land (maximum = 200 km), summed across 16 angular sectors around each coastal cell and was estimated using software developed by Burrows et al. (2008). Wave fetch for each beach (F , $\log_{10}[\text{km}]$) was the \log_{10} transformed value for the cell closest to the sampling station. Openness (O , km^2) was defined as the area of sea connected to a site within a 35 km radius and was calculated from the GSHHS coastal grid according to methods described by Burrows et al. (2010). Tidal range (R , m) for the nearest reference port to each beach was obtained from the UK Hydrographic Office Tide Tables (reproduced by permission of the Controller of Her Majesty's Stationery Office and the UK Hydrographic Office, www.ukho.gov.uk).

Analysis

Analytical approach

Model selection techniques described by Burnham & Anderson (1998) were employed to compare models representing various putative mechanisms controlling growth rate. Sets of candidate models were built around a global model containing all possible terms. Reduced models, lacking specific terms, were then constructed to represent other hypotheses of interest. Model performance was measured using Akaike's Information Criterion (AIC). Small sample correction (AIC_c) was applied when the number of predictors was large compared to the number of observations. Candidate models were compared using AIC differences (Δ_i , the relative Kullback-Leibler difference between a model and the best candidate model) and Akaike weights (ω_i , the likelihood of a candidate model relative to all other candidate models). Burnham & Anderson's (1998) approach for assessing model performance is

that AIC differences of <2, 4 to 7, and >10 indicate 'substantial,' 'considerably less,' and 'essentially no' support for a model, relative to the model with the lowest AIC. Where appropriate, *F*-tests were also performed between nested alternative models, to test for significant differences ($\alpha = 0.05$) in explained variance (Quinn & Keough 2002). Independent and joint contributions of model terms to total explained variance were evaluated with hierarchical partitioning of the r^2 of selected models (Chevan & Sutherland 1991, Mac Nally 1996), using the hier.part package (Walsh & Mac Nally 2008) in R.

Unless explicitly stated, data complied with assumptions for statistical tests. Normality and homoscedasticity were verified visually from plots of raw data and residuals. Collinearity was assessed visually in scatterplot matrices of independent variables. Collinearity was also deemed unacceptably high if variance inflation factors were >10, the condition number >30, or the minimum eigenvalue <0.05 (Quinn & Keough 2002, Hocking 2003).

Spatial and temporal growth variation: unconditional models

Restricted maximum likelihood (REML) models were fitted and compared to identify important scales of spatial and temporal variation in YOY plaice growth rates. Models in this first set included only spatial and temporal random effects and are referred to as 'unconditional models' (Table 1). The global unconditional model (Model a; Table 1) described growth estimates for individual fish (G) as a function of random variation among beaches (S_b), subregions (S_s), regions (S_r), years (Y), the interaction between beaches and years (Y_b), and residual error among individual samples. All but one of the remaining candidate unconditional models (Models b, c, d, f, g; Table 1) lacked single terms. The final candidate unconditional model (Model e) lacked both S_s and S_r to represent the hypothesis that growth varied among beaches and years, without coarser-scale spatial structure. The relative information content of candidate unconditional models gave an indication

Table 1. Models to explain variation in individual growth rates (G) of young-of-the-year European plaice *Pleuronectes platessa*. Unconditional models explained G as random effects of beaches (S_b), subregions (S_s), regions (S_r), years (Y), and the year \times beach interaction (Y_b). Hypothetical models explained growth variation among beaches and years (G_{yb}) as linear functions of day (D), water temperature (trawl- [T_t] and satellite-estimated [T_s]), intra- and interspecific competition (C_c and C_h), and environmental productivity (\log_{10} *Arenicola marina* cast density, P_i ; and \log_{10} chlorophyll *a* concentration, P_p). Exploratory models explained G among beaches (G_{sb}) as linear functions of terms in 'best' or 'global' hypothetical models and additional physical characteristics of beaches: wave fetch (F), openness (O), and tidal range (R). All models contain a residual error term (not shown). Models within each set were compared to assess support for hypotheses

Model structure	Model	Hypothesis
Unconditional models (random effects)		
$G = S_b + S_s + S_r + Y + Y_b$	a	Global unconditional model
$G = S_s + S_r + Y + Y_b$	b	No 'beach' effect
$G = S_b + S_r + Y + Y_b$	c	No 'subregion' effect
$G = S_b + S_s + Y + Y_b$	d	No 'region' effect
$G = S_b + Y + Y_b$	e	No 'subregion' or 'region' effect
$G = S_b + S_s + S_r + Y_b$	f	No 'year' effect
$G = S_b + S_s + S_r + Y$	g	No 'year \times beach' interaction
Hypothetical models		
$G_{yb} = D + T_t + T_s$	h	Maximum growth
$G_{yb} = D + T_t + T_s + C_c$	i	Intraspecific competition
$G_{yb} = D + T_t + T_s + C_h$	j	Interspecific competition
$G_{yb} = D + T_t + T_s + C_c + C_h$	k	Intra- & interspecific competition
$G_{yb} = D + T_t + T_s + P_i + P_p$	l	Productivity
$G_{yb} = D + T_t + T_s + P_i + P_p + C_c$	m	Intraspecific competition & productivity
$G_{yb} = D + T_t + T_s + P_i + P_p + C_h$	n	Interspecific competition & productivity
$G_{yb} = D + T_t + T_s + P_i + P_p + C_c + C_h$	o	Global hypothetical model
Exploratory models		
G_{sb} = Best hypothetical model	p	Best hypothetical model
G_{sb} = Global hypothetical model	q	Global hypothetical model
G_{sb} = Best hypothetical model + $F + O + R$	r	Best hypothetical model & physical characteristics
G_{sb} = Global hypothetical model + $F + O + R$	s	Global hypothetical model & physical characteristics

of the importance of each source of spatial and temporal variation after accounting for the other random effects.

REML models were fitted with the lme4 package (Bates et al. 2011) in R. Average growth estimates by beach (G_{sb}), year (G_y), and beaches by years (G_{yb}), for subsequent analyses, were obtained as best linear unbiased predictors from the best unconditional model. To assess whether fish were growing maximally, these predictors were compared with expected ad libitum growth rates for the temperature range encountered in the field, from previously published laboratory experiments (Ciotti et al. 2010).

Maximum growth and growth limitation hypotheses: hypothetical models

In a second set of candidate models, the ability of the maximum growth/optimal food condition hypothesis to explain variation in growth rate among beaches and years was compared with several alternative hypotheses of food limitation. These models are referred to as 'hypothetical models' (Table 1), since they represented established, *a priori* hypotheses. In the global hypothetical model (Model o; Table 1), average growth rate for beaches by years (G_{yb}) was a linear function of day in August (D), trawl temperature (T_t), satellite-estimated sea surface temperature (T_s), \log_{10} YOY plaice density (C_c), \log_{10} *Crangon crangon* density (C_h), \log_{10} chl *a* concentration in summer (P_p), and \log_{10} *Arenicola marina* cast density (P_i). Trawl temperatures (T_t) are subject to short-term tidal and diel variations that could confound spatial and interannual signals (Ciotti et al. 2010). T_s was therefore included to provide more integrated measurements of temperature. T_t and T_s were correlated (Pearson's $r = 0.31$, $df = 62$; $p = 0.003$) and were collectively considered to describe temperature: no efforts were made to separate short- and long-term temperature effects.

The simplest of the candidate hypothetical models (Model h; Table 1) represented our expectation under maximum growth. This model included $T_t + T_s$ to account for the underlying physiological effect of temperature on growth rate and D to account for additional, unexplained differences among collection dates. Since field temperatures were generally below the optimum for YOY plaice (Fonds et al. 1992, Ciotti et al. 2010), maximum growth would be positively related to temperature. Strictly speaking, Model h would be supported even if some unconsidered factor was limiting growth. Within the bounds of the

processes considered in this study, however, Model h represented the 'null' expectation under maximum growth against which hypotheses of growth limitation (Models i to o; Table 1) were assessed. In models representing growth limitation, the underlying effect of temperature was modified by additional terms representing intraspecific competition (C_c), interspecific competition (C_h), or productivity ($P_p + P_i$). P_p and P_i were correlated (Pearson's $r = 0.48$, $df = 62$; $p < 0.0001$) and were collectively considered to describe productivity: no attempts were made to explore independent effects of these 2 variables. Under food limitation, coefficients for competition terms (C_c and C_h) would be negative, and coefficients for productivity terms (P_p and P_i) would be positive. The various mechanisms of food limitation were not mutually exclusive; intra- and interspecific competition and environmental productivity could all influence growth rate simultaneously (global hypothetical model [Model o; Table 1]). Therefore, candidate hypothetical models represented all possible combinations of growth limitation mechanisms.

Hypothetical models were fitted with ordinary least-squares regression of G_{yb} against standardized independent variables in R and compared with model performance metrics described above. In addition, independent and joint contributions of terms in the global hypothetical model to the overall r^2 were determined with hierarchical partitioning. Finally, F -tests were conducted to test whether models of food limitation (Models i to o; Table 1) explained significantly more variation in growth rate than the basic maximum growth model (Model h; Table 1).

Relationship between growth rate and physical beach characteristics: exploratory models

A third set of candidate models was constructed to explore whether the best hypothetical model was sufficient to explain spatial growth variation, or whether selected physical characteristics of study beaches were also important. These models were referred to as 'exploratory models' (Table 1): although the physical characteristics considered have fundamental influences on abiotic and biotic conditions in plaice nurseries (McLachlan & Brown 2006), we had little basis for *a priori* hypotheses to explain how they would influence growth rate. In the global exploratory model (Model s, Table 1), average growth rate by beach, G_{sb} , was a linear function of across-year averages (by beach, denoted with an apostrophe) of sea surface temperature (T_s'), \log_{10}

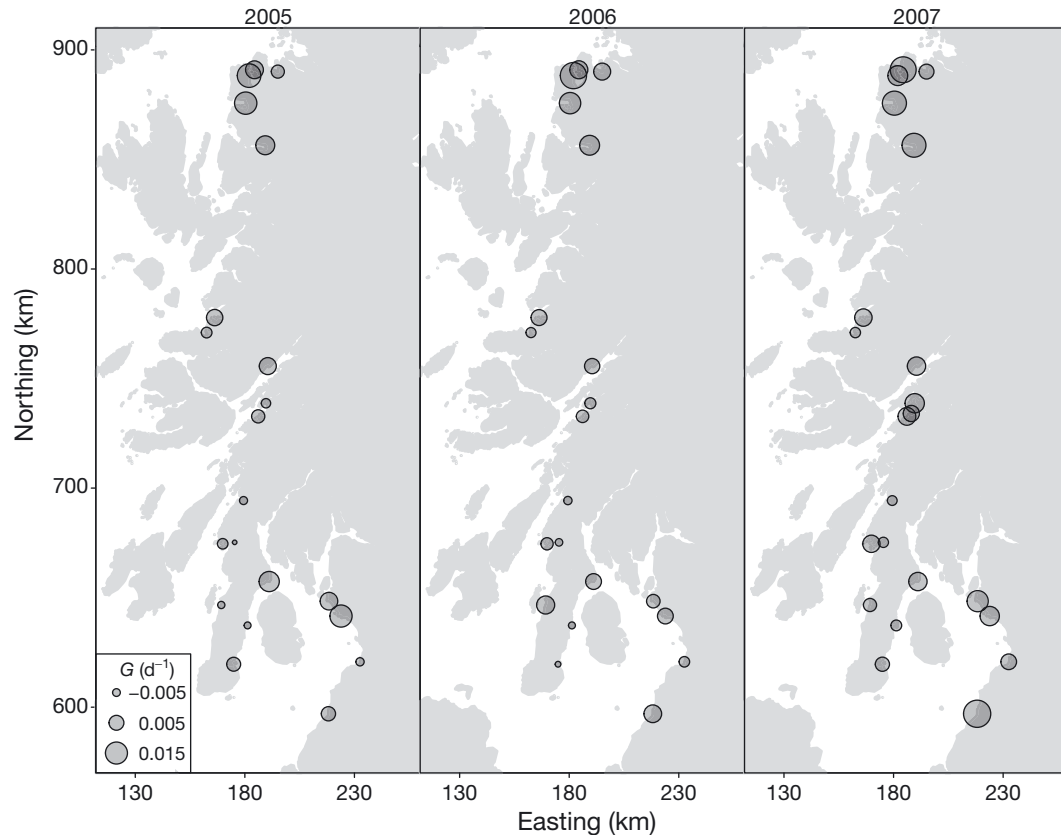


Fig. 2. *Pleuronectes platessa*. Spatial growth variation in young-of-the-year European plaice at beaches in Scotland in mid-August 2005 to 2007. Map features are as in Fig. 1. Symbol size represents best linear unbiased predictions for each beach and year (G_{yb} , d^{-1}) from the best unconditional model (Model e)

YOY plaice density (C_c'), \log_{10} *Crangon crangon* density (C_h'), \log_{10} chl *a* concentration (P_p'), and \log_{10} *Arenicola marina* cast density (P_i'), as well as wave fetch (F), openness (O), and tidal range (R). Additional years of data were included, as available, in across-year averages for some variables (T_s' : 2000 to 2008, P_p' : 2003 to 2008, P_i' : 2001 to 2008). The global exploratory model therefore explained spatial growth variation as a function of all effects of temperature, competitor densities, and environmental productivity examined in the hypothetical models, as well as the 3 physical beach characteristics. Candidate exploratory models were then constructed excluding either the physical beach characteristics (Model q; Table 1), or unimportant hypothetical model terms (Model r; Table 1), or both (Model p; Table 1). In this way, the most successful hypothetical model was double-checked against the global hypothetical model and served as a basic model to assess the importance of physical beach characteristics.

Exploratory models were fitted with ordinary least-squares regression using standardized independent variables in R and compared according to

model performance metrics described above. In addition, independent and joint contributions of terms in the best model to the overall r^2 were determined with hierarchical partitioning. Finally, F -tests were conducted to test whether inclusion of unimportant hypothetical model terms or physical beach characteristics (Models q to s; Table 1) significantly increased variance explained by the best hypothetical model (Model p; Table 1).

RESULTS

Spatial and temporal growth variation: unconditional models

Growth rate of YOY plaice in mid-August varied considerably among the 22 beaches and 3 years. Growth appeared to be faster at beaches in NW Scotland and the Clyde Sea compared to the Kintyre region and faster in 2007 compared to the preceding 2 years (Figs. 1 & 2). Overall, however, variation in average growth rate was high, even among

Table 2. *Pleuronectes platessa*. Relative information content of unconditional models to explain variation in individual growth rates of young-of-the-year European plaice ($n = 791$) at 22 beaches in Scotland. Models were fitted with REML. In the global unconditional model (Model a), individual growth rate (G , d^{-1}), predicted from an RNA-based growth index, varied due to random effects of beaches (S_b), subregions (S_s), regions (S_r), years (Y), and the interaction between beaches and years (Y_b). K : number of predictors including the intercept and a residual error term, AIC: Akaike's Information Criterion, Δ_i : AIC difference, ω_i : Akaike weight for each model. The unconditional model with the lowest AIC is shown in **bold**

Model	Model structure	K	AIC	Δ_i	ω_i
a	$G = S_b + S_s + S_r + Y + Y_b$	7	-4893.6	1.9	0.17
b	$G = S_s + S_r + Y + Y_b$	6	-4889.8	5.8	0.03
c	$G = S_b + S_r + Y + Y_b$	6	-4895.5	0.0	0.45
d	$G = S_b + S_s + Y + Y_b$	6	-4893.8	1.8	0.19
e	$G = S_b + Y + Y_b$	5	-4892.8	2.7	0.12
f	$G = S_b + S_s + S_r + Y_b$	6	-4890.7	4.8	0.04
g	$G = S_b + S_s + S_r + Y$	6	-4843.8	51.7	<0.01

adjacent beaches and among years at the same beach (Figs. 1 & 2).

Growth variation at the level of individual beaches was substantial, but there was little statistical evidence for growth variation among subregions or regions. The relative importance of each source of spatial and temporal growth variation was assessed by comparing the information content of the global unconditional model (Model a) with alternative, nested models (Models b to g; Table 1). Of the 7 candidates compared, the unconditional model lacking subregion (Model c) had the highest information content (Table 2). This model was essentially indistinguishable (low Δ_i and similar ω_i) from several other models (Table 2), namely the global unconditional model (Model a), the model lacking region (Model d), and the model lacking region and subregion (Model e). On the other hand, models lacking beach (Model b), year (Model f), or their interaction (Model g) were highly unlikely and had considerably less, or essentially no, support relative to the model with the lowest AIC (Table 2). In summary, unconditional model comparisons suggested that year, beach, and their interaction were important model terms, but there was no clear evidence for variation at regional or subregional scales. Model e was therefore considered the 'best' unconditional model.

Although growth rates differed substantially among beaches and years, maximum growth was uncommon. G_{Yb} ranged from slightly negative (-0.0095 d^{-1} , Caolisport in 2005) to more substantially positive (0.022 d^{-1} , Girvan in 2007; Fig. 3). In

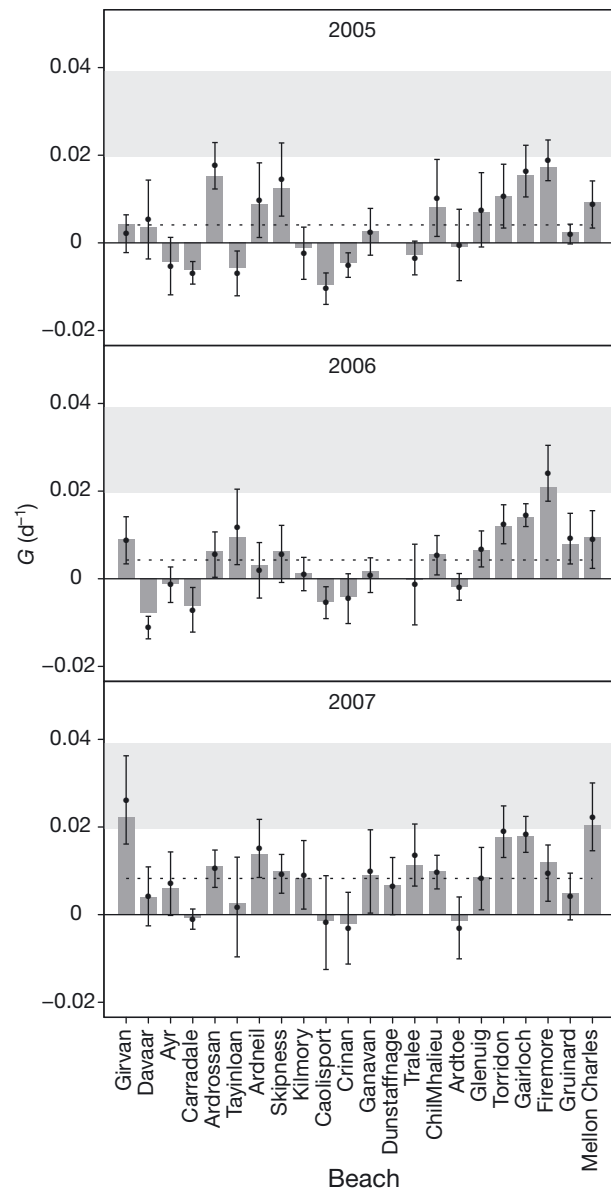


Fig. 3. *Pleuronectes platessa*. Estimated growth rates of young-of-the-year European plaice at beaches in Scotland in mid-August 2005 to 2007, relative to maximum expected rates. Bars are best linear unbiased predictions for each beach and year (G_{Yb}) from the best unconditional model (Model e). Points are means for each beach and year ($\pm 95\%$ confidence limits). Dotted lines are best linear unbiased growth predictions for each year (G_Y) from Model e. The shaded region indicates the maximum range of mean ad libitum laboratory growth rates between 12 and 20°C (Ciotti et al. 2010)

only 3 cases (Firemore 2006, Girvan 2007, and Mellon Charles 2007) did G_{Yb} fall within the range of expected ad libitum growth rates (Fig. 3). Overall, annual growth estimates (G_Y) were higher in 2007 (0.0083 d^{-1}) than in 2005 (0.0041 d^{-1}) or 2006

Table 3. *Pleuronectes platessa*. Relative information content and significance of hypothetical models of maximum growth (Model h) and growth limitation (Models i–o) in young-of-the-year European plaice at 22 beaches in Scotland. Best linear unbiased predictions of growth rate for each beach and year (G_{yb} , d^{-1} , $n = 63$) from the best unconditional model (Model e) were fitted to standardized independent variables using ordinary least-squares regression. All models are defined as in Table 1. The hypothetical model with the lowest AIC_c (Akaike's Information Criterion corrected for small sample size) is shown in **bold**. Further parameters as in Table 2. Significance of growth limitation models relative to the null hypothesis of maximum growth (Model h) was tested with *F*-tests (df, p). na: not applicable

Model	Model structure	<i>K</i>	AIC _c	Δ_i	ω_i	df	p
h	$G_{yb} = D + T_i + T_s$	5	−431.4	10.2	<0.01	0	na
i	$G_{yb} = D + T_i + T_s + C_c$	6	−440.1	1.6	0.16	1	0.0015
j	$G_{yb} = D + T_i + T_s + C_h$	6	−432.8	8.8	<0.01	1	0.0610
k	$G_{yb} = D + T_i + T_s + C_c + C_h$	7	−441.1	0.6	0.26	2	0.0013
l	$G_{yb} = D + T_i + T_s + P_i + P_p$	7	−434.5	7.1	<0.01	2	0.0263
m	$G_{yb} = D + T_i + T_s + P_i + P_p + C_c$	8	−441.6	0.0	0.34	3	0.0011
n	$G_{yb} = D + T_i + T_s + P_i + P_p + C_h$	8	−433.7	8.0	<0.01	3	0.0318
o	$G_{yb} = D + T_i + T_s + P_i + P_p + C_c + C_h$	9	−440.7	0.9	0.22	4	0.0016

(0.0043 d^{-1} ; Fig. 3). Therefore, despite high variability in growth rate among beaches and years, growth of YOY plaice in mid-August was generally slow, had ceased altogether in some cases, and rarely attained rates measured under ad libitum feeding conditions in the laboratory.

Growth rates and total lengths of individual fish were positively correlated (Pearson's $r = 0.54$, $df = 788$; $p < 0.0001$). This positive correlation was evident not only within (correlation between residuals from Model g and total length, Pearson's $r = 0.47$, $df = 788$; $p < 0.0001$), but also among beaches and years (Pearson's r between average growth rate and total length by beach and year = 0.52, $df = 62$; $p < 0.0001$).

In summary, examination of unconditional models suggested that growth variation at the level of individual beaches and years was substantial, but provided no evidence for growth variation among subregions or regions. In addition, average growth rate by beach and year only occasionally approached maximum rates. Finally, growth rate was positively correlated with body size, both among and within beaches.

Maximum growth and growth limitation hypotheses: hypothetical models

Causes of growth variation were examined by regressing average growth rate by beach and year (best linear unbiased predictors from Model e: G_{yb}) against environmental variables. The maximum growth model was compared to several models describing alternative hypotheses of growth limitation due to intra- and interspecific competitor densities and environmental productivity (Table 1). The

hypothetical model including intraspecific competitor density and productivity metrics (Model m) had the highest information content (Table 3). There was substantial support ($\Delta_i \leq 1.58$), and high relative likelihood ($\omega_i = 0.16$ to 0.26) for all other hypothetical models that included \log_{10} YOY plaice density (Models i, k, and o), regardless of whether productivity metrics or \log_{10} *Crangon crangon* density were included (Table 3). On the other hand, models including \log_{10} *C. crangon* density (Model j), productivity metrics (Model l), or both (Model n) had less support ($\Delta_i = 7.15$ to 8.81) and very low relative likelihoods ($\omega_i \leq 0.0097$) if \log_{10} YOY plaice density was not included (Table 3). There was essentially no support, and the lowest likelihood of all, for the maximum growth model (Model h; Table 3). In addition, the maximum growth model explained significantly less variation in growth rate than almost all of the other hypothetical models examined (Table 3). Therefore, model comparisons suggested that after accounting for effects of temperature and day, there was an effect of intraspecific competitor density but not interspecific competitor density or environmental productivity on growth variation among beaches and years.

The importance of variables explaining growth variation among beaches and years was assessed by hierarchical partitioning of the global hypothetical model (Model o). Intraspecific competitor density (C_c) clearly made the largest independent contribution, and almost no joint contribution, to explained variance in growth rate (Fig. 4). Day (D) and trawl temperature (T_i) made moderate independent contributions and low joint contributions (Fig. 4). Metrics of productivity (P_p and P_i) made moderate independent contributions, but also moderate joint contributions (Fig. 4). Joint contributions for P_p and P_i may have

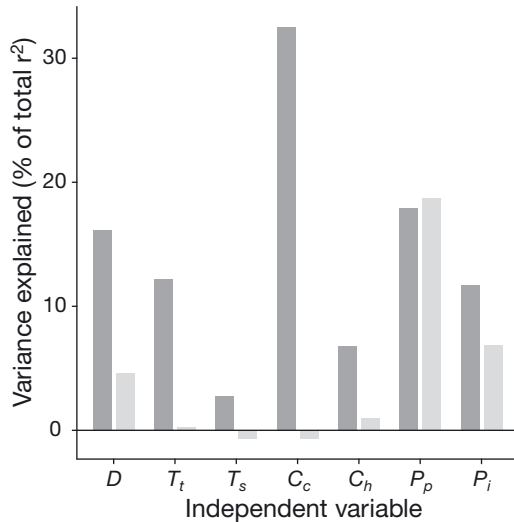


Fig. 4. *Pleuronectes platessa*. Importance of independent variables in the global hypothetical model (Model o) explaining growth variation of young-of-the-year European plaice ('YOY plaice') among beaches and years. In Model o, best linear unbiased predictions of growth rate for each beach and year (G_{yb} , d^{-1} , $n = 63$) from the best unconditional model (Model e) were fitted to sampling day (D), trawl temperature (T_t), sea surface temperature (T_s), \log_{10} YOY plaice density (C_c), \log_{10} *Crangon crangon* density (C_h), \log_{10} *Arenicola marina* cast density (P_i), and \log_{10} chlorophyll *a* concentration (P_p) using ordinary least-squares linear regression. Bars represent relative independent (dark grey) and joint (light grey) contributions of each variable to total independent r^2 , determined by hierarchical partitioning

resulted from collinearity between these variables (Pearson's $r = 0.48$, $df = 62$; $p < 0.0001$). However, it is unlikely that collinearity was the reason why effects of productivity were not detected during model selection, because diagnostics of collinearity were within acceptable bounds and conclusions were identical when the analyses were re-run including only the most important productivity metric (P_p). Contributions due to interspecific competitor density (C_h) and sea surface temperature (T_s) were small (Fig. 4). In summary, hierarchical partitioning supported the finding from AIC_c-based model comparisons: intraspecific competitor density best explained YOY plaice growth rates.

Examining the regression coefficients from the global hypothetical model (Model o) provided further insights. Growth rate was inversely related to intraspecific competitor density (C_c ; slope \pm SE: -0.00266 ± 0.000874 , $t = -3.04$; $p = 0.0036$) consistent with the hypothesis of growth limitation due to competition. Coefficients for trawl temperature (T_t ; 0.00172 ± 0.00101 , $t = 1.69$; $p = 0.096$) and day (D ; -0.00170 ± 0.000909 , $t = -1.87$; $p = 0.067$) were marginally non-significant,

providing weak evidence that growth rate was faster at higher temperatures and declined throughout August. Coefficients for sea surface temperature (T_s ; 0.000471 ± 0.000993 , $t = 0.475$; $p = 0.64$), intertidal benthic productivity (P_i ; -0.00137 ± 0.00101 , $t = -1.36$; $p = 0.18$), nearshore primary productivity (P_p ; -0.000858 ± 0.00107 , $t = -0.800$; $p = 0.43$), and interspecific competitor density (C_h ; -0.00119 ± 0.000941 , $t = -1.27$; $p = 0.21$) were not significant. Negative coefficients for both productivity metrics were clearly inconsistent with the hypothesis of faster growth in more productive environments.

In summary, examination of hypothetical models supported the hypothesis that intraspecific competition, and not temperature, interspecific competition, or environmental productivity, controls mid-August growth rates of YOY plaice in west Scotland. Model i was considered the 'best' hypothetical model (Table 3).

Relationship between growth rate and physical beach characteristics: exploratory models

The final set of candidate models explored whether intraspecific competitor density and temperature were sufficient to explain variation in growth rate among beaches or whether physical characteristics might also be important. Mean values and among-beach variability of independent variables are provided in Table 4. The structure of the best hypothetical model (Model i) was used to define the basic model for exploratory analyses. This basic exploratory model explained average growth rate by beach (G_{sb}) as a linear function of average sea surface tempera-

Table 4. Mean values and among-beach variability of independent variables, including sea surface temperature (T_s' , °C), \log_{10} young-of-the-year European plaice *Pleuronectes platessa* density (C_c' , $\log_{10}[\text{ind. m}^{-2}]$), \log_{10} *Crangon crangon* density (C_h' , $\log_{10}[\text{ind. m}^{-2}]$), \log_{10} *Arenicola marina* cast density (P_i' , $\log_{10}[\text{casts m}^{-2}]$), \log_{10} chlorophyll *a* concentration (P_p' , $\log_{10}[\text{mg m}^{-3}]$), wave fetch (F , $\log_{10}[\text{km}]$), openness (O , km^2), and tidal range (R , m)

Independent variable	Mean	SD
T_s'	12.7	0.728
C_c'	-0.982	0.245
C_h'	0.00938	0.530
P_p'	0.139	0.120
P_i'	0.0635	0.862
F	2.17	0.739
O	1077	403
R	2.37	0.739

Table 5. *Pleuronectes platessa*. Relative information content and significance of exploratory models to explain growth variation in young-of-the-year European plaice at 22 beaches in Scotland. Candidate exploratory models include 2 hypothetical models before (Models p and q) and after (Models r and s) inclusion of 3 independent variables representing physical beach characteristics. In each model, best linear unbiased predictions of growth rate for each beach (G_{Sb} , d^{-1} , $n = 22$) from the best unconditional model (Model e) were fitted to standardized independent variables using ordinary least-squares regression. All models are defined as in Tables 1 & 4. The exploratory model with the lowest AIC_c (Akaike's Information Criterion corrected for small sample size) is shown in **bold**. Further parameters as in Table 2. Significance of candidate exploratory models relative to the basic hypothetical model (Model p) was tested with F -tests (df, p). na: not applicable

Model	Model structure	K	AIC_c	Δ_γ	ω_γ	df	p
p	$G_{Sb} = T_s' + C_c'$	4	-166.9	8.5	0.01	0	na
q	$G_{Sb} = T_s' + C_c' + C_h' + P_p' + P_i'$	7	-163.8	11.7	<0.00	3	0.095
r	$G_{Sb} = T_s' + C_c' + F + O + R$	7	-175.4	0.0	0.98	3	0.002
s	$G_{Sb} = T_s' + C_c' + C_h' + P_p' + P_i' + F + O + R$	10	-159.8	15.6	<0.01	6	0.019

ture (T_s') and average \log_{10} intraspecific competitor density (C_c' ; Model p; Table 5). This model did not include trawl temperatures (T_t), since T_s' was considered a better metric of average temperature conditions. Sampling day (D), which varied for each beach among years, was also omitted since exploratory analyses focused on explaining averaged spatial variation across years. The basic exploratory model explained 33 % of growth variation among beaches. As expected, including interspecific competitor density and environmental productivity (the unsuccessful hypothetical model terms; Model q) did not significantly increase the variance explained of the basic model (Table 5). On the other hand, explained variance was significantly increased by inclusion of the 3 physical beach characteristics (Model r; Table 5). Of the 4 candidate exploratory models compared, the model including the 3 physical characteristics (Model r) had the highest information content (Table 5). Relative to Model r, there was essentially no support for exploratory models that either lacked physical beach characteristics (Model p) or included the other indices of competition and environmental productivity (Model s) or both (Model q). The weight of evidence (ω_γ) was 98 % in favor of the best model (Model r), 1.4 % in favor of the basic model (Model p), and less than 0.3 % in favor of either model including the unsuccessful hypothetical model terms (Models q and s; Table 5). Therefore, examination of growth variation among beaches supported the previous finding that interspecific competition, intertidal benthic productivity, and nearshore primary productivity do not explain growth variation of YOY plaice. One or more of the 3 physical beach characteristics explored were, however, important.

The 5 independent variables in the best exploratory model (Model r) collectively explained 73 % of the variation in growth rate among beaches (F -test, df =

5, 16; $p = 0.0004$). Hierarchical partitioning suggested that 75 % of this explained variance was due to independent contributions of \log_{10} YOY plaice density and tidal range (Fig. 5). Interestingly, tidal range (independent contribution = 52 %) was apparently more important than intraspecific competitor density (independent contribution = 23 %). Joint contributions were generally small compared to independent contributions. Although there was a negative coefficient for \log_{10} YOY plaice density (Fig. 6), consistent with the intraspecific competition hypothesis, this coefficient

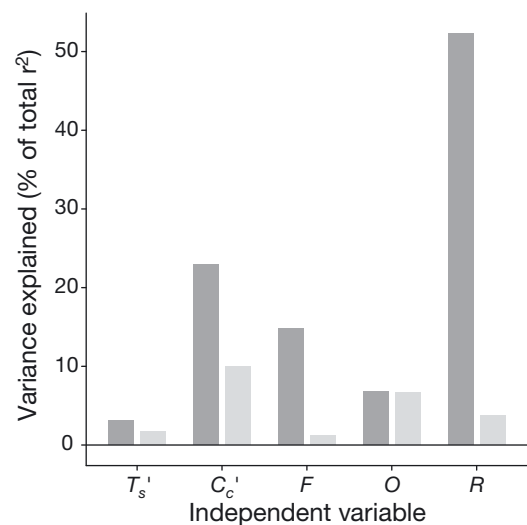


Fig. 5. *Pleuronectes platessa*. Importance of independent variables in the best exploratory model (Model r) explaining growth variation of young-of-the-year European plaice among beaches in mid-August. In Model r, best linear unbiased predictions of growth rate for each beach (G_{Sb} , d^{-1} , $n = 22$) from the best unconditional model (Model e) were fitted to T_s' , C_c' , F , O and R using ordinary least-squares linear regression. All variables defined as in Table 4. Bars are relative independent (dark grey) and joint (light grey) contributions of each variable to total independent r^2 , determined by hierarchical partitioning

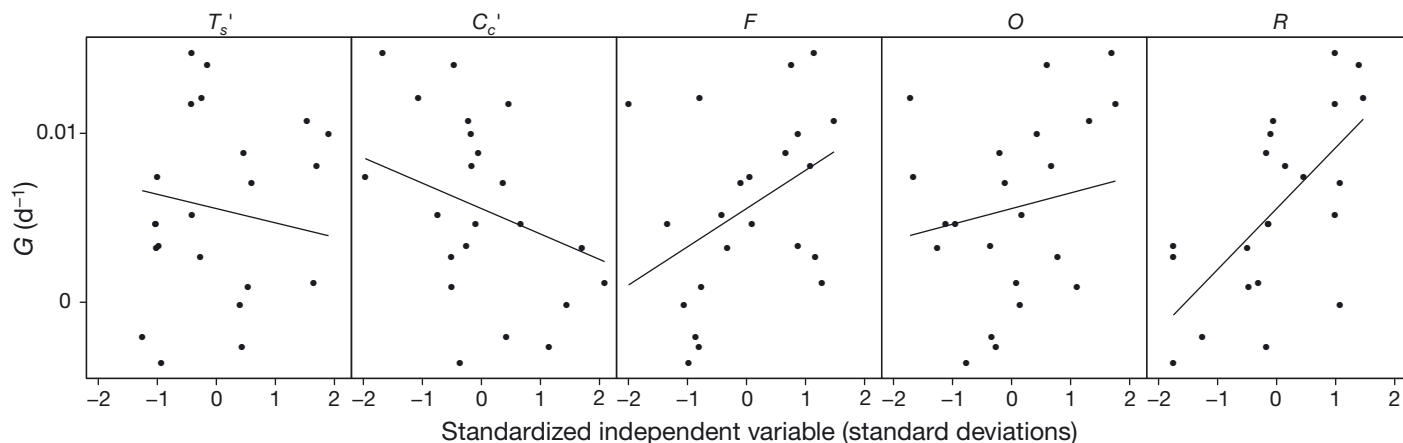


Fig. 6. *Pleuronectes platessa*. Relationship between mid-August growth rates of young-of-the-year European plaice and independent variables at beaches in Scotland. Observed average growth rates for each beach (points, G_{sb}) and partial regression slopes from the best exploratory model (Model r , lines) are plotted against T_s' , C_c' , F , O , and R (all variables defined as in Table 4). Independent variables are standardized to mean 0 + 1SD

cient was marginally non-significant (slope \pm SE: -0.00150 ± 0.000797 , $t = 1.88$; $p = 0.077$). On the other hand, there were significant positive coefficients for tidal range (0.00361 ± 0.000776 , $t = 4.65$; $p = 0.0003$) and wave fetch (0.00226 ± 0.000891 , $t = 2.54$; $p = 0.022$; Fig. 6). Growth rate was not significantly related to openness or sea surface temperature (Fig. 6). Therefore, although exploratory analyses provided some support for the intraspecific competition hypothesis, there was greater evidence for effects of physical characteristics. In general, fish grew faster at beaches with larger tidal range and wave fetch.

Variation in tidal range at large scales, modified by local effects of YOY plaice density and wave fetch, best explained spatial growth patterns. Tidal range varied along the west coast of Scotland at broad spatial scales that appeared to correspond well with regional variation in growth (Figs. 2 & 7). Growth variation within these broad regions was sometimes related to \log_{10} YOY plaice density (Fig. 7). For example, both tidal ranges and growth rates were high in NW Scotland, low in Kintyre, and intermediate in the Clyde Sea (Fig. 7). However, all beaches in the Clyde Sea had similar tidal range and supported rapid growth, with the exception of 2 with unusually high YOY plaice densities (Ayr and Carradale, Fig. 7). Wave fetch also appeared to explain some of the variation within the western Clyde subregion and the Kintyre and Moidart regions (Fig. 7). Fig. 7 therefore suggests that variation in tidal range may influence growth rate at large spatial scales, but influences of wave fetch and conspecific density would operate more locally.

In summary, examination of exploratory models suggested that the hypothesis of intraspecific competition explained growth variation among beaches, but physical beach characteristics (particularly tidal range and wave fetch) were also important. Cartographic representations (Fig. 7) suggested that growth rate was related to tidal range at broad scales and to wave fetch and intraspecific competition at small spatial scales.

DISCUSSION

By focusing on 22 locations spread over ca. 300 km of coastline in west Scotland, this study provides the most spatially-extensive investigation of variation in short-term growth rate of YOY plaice to date. Growth variation at the level of individual beaches and years was substantial, but there was little evidence for growth variation among subregions or regions (findings from 'unconditional model' comparisons). Average growth rate by beach and year only occasionally approached maximum rates. Among beaches and years, the hypothesis that intraspecific competition was responsible for growth variation was supported, but there was no evidence for roles of interspecific competition, environmental productivity or temperature (findings from 'hypothetical model' comparisons). Intraspecific competition also explained overall growth variation among beaches, but physical beach characteristics, particularly tidal range and wave fetch, were just as important (findings from 'exploratory model' comparisons).

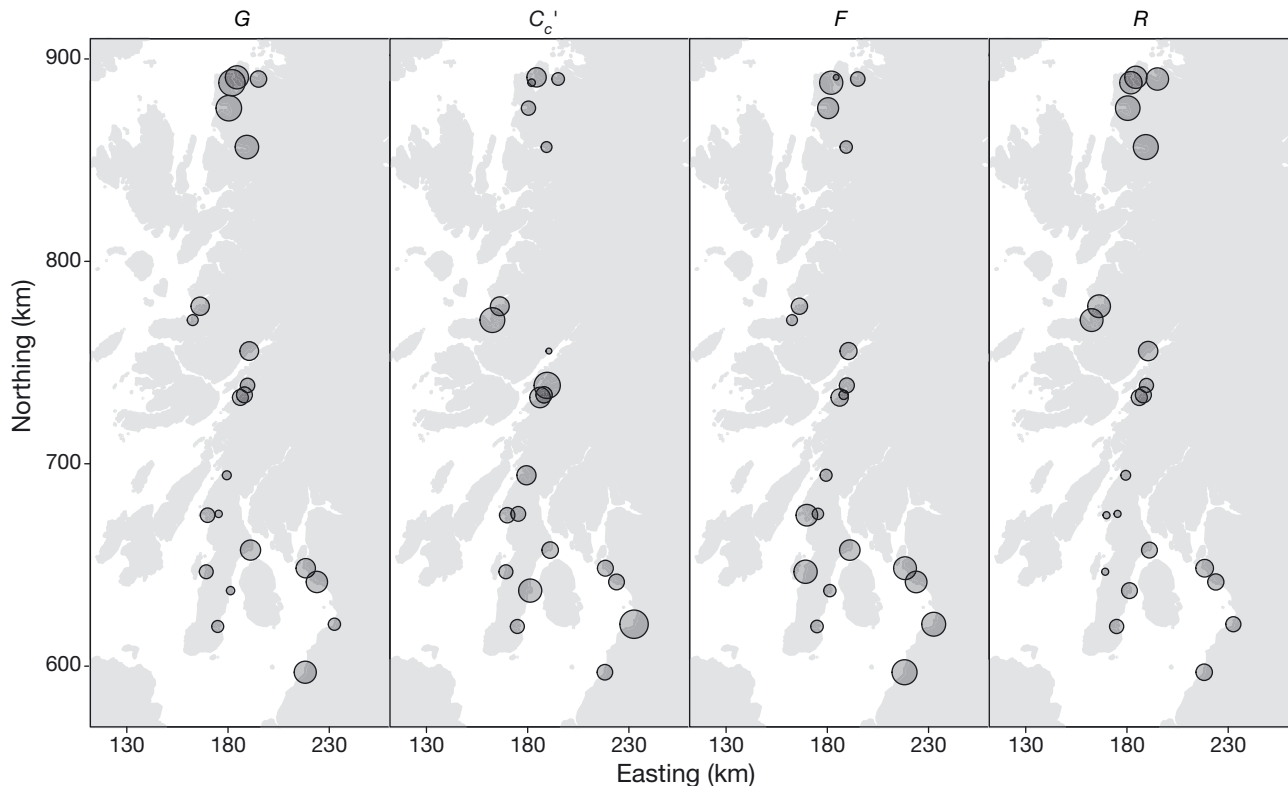


Fig. 7. *Pleuronectes platessa*. Young-of-the-year European plaice ('YOY plaice') growth rate (G_{sb}), \log_{10} YOY plaice density (C_c'), wave fetch (F), and tidal range (R) at beaches in Scotland. Map features are as in Fig. 1. Point sizes represent variable values, standardized to mean 0 + 1SD. Growth rates (G_{sb}) are best linear unbiased predictions for each beach from the best unconditional model (Model e). \log_{10} YOY plaice densities are averages of the 3 study years

Many factors affect the selection of an appropriate growth and condition metric, including cost, logistical constraints, the ecological question, and the spatial and temporal scale of investigation. Variability in RNA:DNA ratios of YOY plaice in Galway Bay led De Raedemaeker et al. (2012) to suggest that this metric is less suitable than more stable, less temporally responsive morphometric indices to assess juvenile fish condition and nursery habitat quality. We argue that recognizing temporal variability relative to dynamic environmental conditions is critical to determining the causes of spatial growth variation in young fishes (Brandt & Mason 1994). Shorter-term growth estimates are less likely to accumulate confounding influences of previous conditions and can be more directly linked to synoptic environmental variables. Furthermore, there is an association between temporal and spatial scales such that fine temporal resolution produces fine spatial resolution (Wiens 1989, Pittman & McAlpine 2003). The need for fine resolution is especially critical in shallow, inshore areas characterized by high environmental heterogeneity (Stierhoff et al. 2009). Our RNA-based approach provided relatively fine-resolution esti-

mates of individual growth rate (Ciotti et al. 2010). Furthermore, since growth could be estimated rapidly (thus in large numbers of individuals), it was possible to study many nurseries covering a broad stretch of coastline. Therefore, our careful efforts to develop and validate a novel nucleic acid index (Ciotti et al. 2010) provided some considerable advantages in achieving an understanding of growth dynamics within a fine-grained, spatially-extensive framework.

Direct, RNA-based estimates of individual growth also avoid measurement biases associated with size-frequency progression analyses that result from systematic changes in size distributions through processes other than growth, such as settlement, emigration, or mortality. RNA-based techniques are robust to these selective processes, reflecting their influences on growth rate but not on the estimation of growth rate. These selective processes could be important causes of growth variation in young plaice: for example, enrichment of populations with slower-growing phenotypes during the summer, through emigration or mortality of larger (faster growing) individuals, could produce spatial variation in growth rate if

mortality or emigration conditions varied between beaches. However, a previous study of nursery beaches on the west coast of Scotland (Ciotti et al. in press) found little evidence to support this possibility.

Unconditional model comparisons detected growth variation among beaches (25 km scale) and years, but not among subregions (50 km scale) or regions (100 km scale). Variation in growth rates among adjacent beaches and consecutive years appeared to be considerable (Figs. 2 & 3). Therefore, the current study provides substantial evidence that growth of YOY plaice is highly dynamic within and among beaches. It remains possible that regional- and sub-regional-scale variation is superimposed on these local dynamics, even though this possibility was not supported by our unconditional model comparisons. Informal simulations (not shown) suggested that our model selection framework was relatively conservative at detecting regional and subregional variation. Furthermore, average growth rates did appear to differ at regional scales (Figs. 2 & 3). Overall, however, the apparent importance of variation among and within individual beaches supports the concept of 'mini-nurseries' (Beverton & Iles 1992) whereby coastal regions used by a single population are subdivided into vast numbers of heterogeneous units, each with different functional attributes.

Growth rates in mid-August in the current study were sometimes negative. While applications of RNA-based indices are subject to some biases, they are considered broadly capable of distinguishing among growth conditions in plaice nurseries, and the existence of negative growth in the late summer has been supported by direct growth measurements of caged individuals (Ciotti et al. 2010, Ciotti 2012). In fact, our RNA-predicted growth rates correspond reasonably well with previous estimates available at some of the study beaches. Increments in total length at Firemore Bay in August ranged from 0.16 to 0.2 mm d⁻¹ ($G = 0.0096$ to 0.012 d⁻¹, assuming $L_T = 50$ mm; Steele & Edwards 1970). In a later study, increments in total length in August were 0.25 mm d⁻¹ at Firemore Bay and 0.35 mm d⁻¹ at Ayr ($G = 0.015$ and 0.018 d⁻¹, respectively; Poxton et al. 1983).

Our benchmarks for maximum growth did not account for allometric scaling relationships between instantaneous growth rate and body size (Fonds et al. 1992). This was a simplifying assumption, and probably did not greatly influence our conclusions. Maximum growth benchmarks were most likely conservative (Ciotti et al. 2010) and were developed using fish that corresponded closely with the range of sizes in the current study.

Relative differences in body size were also insufficient to explain observed variation in growth rate as a consequence of body mass scaling. Average total length for each beach and year ranged from 40.38 to 74.49 mm. Assuming a mass-scaling coefficient of -0.25 (Fonds et al. 1992), body size allometry would produce growth rates ranging from 0.0045 to 0.0075 d⁻¹ if fish were growing at 0.006 d⁻¹ on average. Observed G_{yb} , on the other hand, was much more variable, ranging from -0.0095 to 0.022 d⁻¹. In fact, growth was positively related to body size across beaches and individuals. Therefore, there is little evidence that allometric effects of body size on growth rate explain observed growth variations.

Despite estimating growth rates of YOY plaice in multiple years and at numerous beaches spanning a long stretch of coastline in west Scotland, instances of maximum growth were rare. This study therefore adds substantially to a growing body of evidence refuting the maximum growth/optimal food condition hypothesis (*sensu* Karakiri et al. 1991, van der Veer & Witte 1993) as a general explanation for YOY plaice growth dynamics. As noted by Ciotti et al. (in press), previous reports of maximum growth are often restricted to the early summer (Zijlstra et al. 1982, van der Veer 1986, van der Veer et al. 1990, Amara et al. 2001). Detailed investigations of temporal dynamics indicate that growth often becomes limited in the late summer (Jager et al. 1995, Teal et al. 2008, Freitas et al. 2010, van der Veer et al. 2010, Ciotti et al. in press), at which point maximum growth is the exception, rather than the rule.

The current study supports previous findings of positive relationships between size and individual growth rate in YOY plaice at interindividual and spatial scales (Nash et al. 1994, Ciotti et al. in press). Interestingly, this relationship is negative at temporal scales: growth rate declines, but body size increases during the summer (van der Veer et al. 2010, Ciotti et al. in press). We suggest 2 possible reasons for the positive relationship we observed in the current study. First, body size is partially determined by long-term growth rate and may reflect short-term growth signals if growth is relatively consistent. Second, larger size may facilitate faster growth by providing advantages in competitive interactions, diet, or metabolic efficiency *in situ*. Size influences habitat use, prey profitability, and behavior of young fish (Werner et al. 1983) with likely consequences for growth rate (Huss et al. 2008). YOY plaice eat larger items as they grow (Lockwood 1984) and will therefore experience a progression in the availability and profitability of prey even if the prey community

remains constant. The mechanism underlying the positive relationship between body size and growth rate of YOY plaice at spatial and interindividual scales requires clarification.

The current study supported the hypothesis that growth variation resulted from intraspecific competition. An inverse relationship between density and growth rate was documented previously during manipulative experiments with YOY plaice and 1 of their most important prey items, the bivalve *Angulus tenuis* (da Costa) (previously, *Tellina tennis*), at Firemore Bay, Scotland (Edwards et al. 1970, Trevallion et al. 1970). Field observations at this beach over 4 yr indicated that YOY plaice grew slowest in the year with highest conspecific densities (Steele et al. 1970). A similar association between years of slow growth and high density was later documented in other areas including the Clyde Sea, Scotland (Poxton et al. 1983), Torseröd Bay, Sweden (Modin & Pihl 1994), Port Erin Bay, Isle of Man (Nash et al. 1994, 2007), Ardmucknish Bay, Scotland (Nash et al. 2007), and the southern coasts of the North Sea (Rijnsdorp & van Leeuwen 1996, Teal et al. 2008). Therefore, all previous evidence for density dependence is from interannual comparisons at a single location. Growth rates of fish in the present study were also faster in the year (2007) with the lowest density.

The current study, however, provides the first evidence for spatial density dependence of YOY plaice growth rates. Some previous studies examining spatial growth variation focused on food conditions and did not address the possibility of intraspecific competition (Berghahn 1987, Karakiri et al. 1989, Berghahn et al. 1995). However, studies in west Scotland (Ciotti et al. in press), southwest Ireland (Haynes et al. 2012), and the Dutch Wadden Sea (van der Veer & Witte 1993) found no evidence for spatial density dependence despite being designed to test this possibility.

There are several possible reasons why we detected spatial density dependence but previous studies did not. First, the relationship between growth rate and density in the current study was relatively weak: large sample sizes or extensive surveys may be required to separate the density 'signal' from environmental and methodological 'noise.' Second, growth may only be limited by intraspecific competition in areas with particularly high YOY plaice densities or low carrying capacities. In British bays, YOY plaice densities are thought to be higher than in the Wadden Sea (Pihl & Rosenberg 1982), but still reach carrying capacity only occasionally (Nash et al. 2007). Third, since growth limitation may be more

prominent in late summer (Ciotti et al. in press), density dependence may not be detected in integrated estimates of seasonal growth (Teal et al. 2008). Finally, it is possible that a relationship between density and growth rate was masked in previous studies due to spatial scale- or context-dependent processes such as the ideal free distribution (Power 1983, 1984). In the Dutch Wadden Sea, an extensive, nearly continuous ca. 1000 km² tidal flat, aggregations of fish in areas with high prey abundance may have masked negative impacts of density on growth rate (van der Veer & Witte 1993). We found no correlation between YOY plaice density and metrics of productivity in west Scotland (data not shown), possibly because beaches were punctuated by long stretches of unsuitable, rocky, intertidal habitat which restricted along-shore movement and prevented individuals from distributing 'freely.'

Growth rates in the present study were related to YOY plaice densities but not to metrics of productivity. This implies that competition was for some resource other than food, or that it operated through interference. This is unexpected because manipulative experiments at Firemore Bay (Scotland) provided evidence that YOY plaice do compete for food: YOY plaice growth rates in mesocosms depended on the ratio of YOY plaice to their prey rather than on absolute YOY plaice density (Trevallion et al. 1970). Other studies have found relationships between YOY plaice growth rates and food resources under natural conditions (Poxton et al. 1983, van der Veer & Witte 1993, Berghahn et al. 1995).

Another possible reason for the absence of a relationship between productivity and growth rate is that our metrics of productivity may not accurately reflect prey conditions available to YOY plaice. In contrast to the Dutch Wadden Sea (van der Veer & Witte 1993), *Arenicola marina* is not an important YOY plaice prey item at beaches on the west coast of Scotland (Edwards & Steele 1968, Poxton et al. 1983). While log₁₀ *A. marina* cast density and log₁₀ chl *a* concentrations were correlated, suggesting that both reflect some common productivity signal, neither YOY plaice growth nor the abundance of important YOY plaice prey items are necessarily related to these general patterns of productivity (Ciotti 2012).

Despite evidence for intraspecific competition, densities of the interspecific competitor (*Crangon crangon*) were not related to YOY plaice growth rates in this study. Besides YOY plaice, dominant epibenthic macrofauna on shallow, moderately exposed beaches in northwest Europe include *C. crangon*, *Pomatoschistus* sp., and *Carcinus maenas* (L.) (Pihl &

Rosenberg 1982, Gibson et al. 1993, Amara & Paul 2003). Of these, *C. crangon* are probably the most important YOY plaice competitors due to their high abundance and diet overlap with YOY plaice (Evans 1983, Pihl 1985). Although other flatfishes, such as common dab *Limanda limanda* (L.) (Gibson et al. 1993), sometimes reach high densities on plaice nursery beaches, niches are probably segregated by seasonality, diel period, spatial distribution, and/or prey preferences (Ansell & Gibson 1990, Besyst et al. 1999, Amara et al. 2001). The lack of evidence for interspecific competition is therefore surprising, especially since *C. crangon* densities were an order of magnitude higher than YOY plaice densities (Table 4). Several factors could reduce competition among heterospecifics relative to conspecifics, including partitioning of the diet (Evans 1983) or the temporal or spatial niche (Gibson et al. 1998), or competition through non-exploitative processes, such as interference. It is also possible that densities of *C. crangon* were too small or invariable to create measurable impacts on growth rate or that growth or density signals were too noisy to detect them.

Interestingly, spatial growth variation in this study was related to general physical characteristics of beaches. Analyses were exploratory and do not permit strong conclusions, especially given the small sample size (22 beaches) and the large number of predictor variables (Anderson et al. 2001). Exploratory analyses were, however, useful in generating new hypotheses for future testing. Of the variables considered, tidal range explained most growth variation among beaches. The positive influence of tidal range on growth may stem from its influence on density. Short-term growth rate at a given time most likely responds to density conditions integrated over all tidal stages ('effective density'). However, 'observed densities' in the current study were measured only at low tide. If beach slope is constant, larger tidal ranges are translated to wider intertidal areas, greater dilution of low tide densities at high tide, and thus greater differences between observed and effective densities. Tidal range would have a particularly large positive influence on growth rate if effective density is disproportionately weighted by processes operating at high tide: if, for example, YOY plaice are competing for prey and other resources in the intertidal zone. It remains unknown whether the association between tidal range and YOY plaice growth rates in our study has broader spatial relevance.

Growth rates of YOY plaice were also positively related to wave fetch. The positive association be-

tween these 2 variables is surprising, firstly because the biomass and diversity of macrobenthic infauna decrease (McIntyre & Eleftheriou 1968, McIntyre et al. 1970, Eleftheriou & McIntyre 1976) and predator biomass increases (Pihl & van der Veer 1992) with increasing exposure, and secondly because wave action is thought to inhibit feeding in YOY plaice (Steele et al. 1970, Lockwood 1980, 1984). It is possible that turbulence due to waves actually reduces predator avoidance by prey (Gabel et al. 2011). Wave exposure can also influence sediment properties, a potentially important determinant of habitat quality for young flatfish (Gibson 1994). Another possibility is that wave fetch, along with tidal range and YOY plaice abundance, mediates the intensity of intraspecific competition: if sediment particle size is constant, more exposed beaches have flatter slopes, larger intertidal areas (McLachlan & Brown 2006), and therefore lower YOY plaice densities at high tide.

In conclusion, this study demonstrates that the maximum growth/optimal food condition hypothesis can nearly always be rejected for YOY plaice in August at beaches along the west coast of Scotland and that growth is limited by intraspecific competition. However, this explanation accounts for relatively little variance in growth rate among individuals and beaches, and temporal reductions in growth rate during late summer require other explanations entirely (Nash et al. 1994, Ciotti et al. in press). Processes underlying growth variation are apparently complex.

Several processes require further investigation. The interaction between YOY plaice feeding and the dynamics of specific prey types may be critical (Ciotti 2012). It may also be necessary to account for the dependence of this interaction on body size, abiotic variables, and competitor or predator assemblages. In particular, very few studies have examined whether growth variation in YOY plaice is related to predation risk even though this factor may be a critical determinant of feeding and growth in young fishes such as YOY plaice (Burrows et al. 1994, Burrows & Gibson 1995, Ryer & Hurst 2008). In addition, the extent to which spatial growth variation is driven by differences in growth performance through genetic or non-genetic local adaptation requires testing. Finally, the present study indicated that physical beach characteristics, such as tidal range and wave fetch, were important in explaining spatial growth variation. These physical characteristics probably have overarching influences on patterns of habitat use as well as the abiotic (turbulence, temperature, turbidity) and biotic (prey, competitors, predators,

larval supply) features of plaice nurseries. More detailed assessments of relationships and underlying mechanisms linking YOY plaice growth rates with these physical variables would be a promising direction for future research. In particular, the hypothesis that tidal range and wave fetch both influence growth rate by mediating effective competitor densities requires testing.

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