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Habitat characteristics promoting high density and condition of juvenile flatfish at nursery grounds on the west coast of Ireland

F. De Raedemaecker *, D. Brophy, I. O'Connor, S. Comerford

Marine and Freshwater Research Centre, Department of Life and Physical Sciences, Galway-Mayo Institute of Technology, Dublin Road, Galway, Ireland

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ABSTRACT

Coastal zones are essential nursery habitats for most juvenile flatfish species. Understanding the habitat requirements promoting high abundance and growth of juvenile flatfish is important for evaluating nursery habitat quality. The present study aimed to assess nursery ground quality for the most common flatfish species: dab (*Limanda limanda*) and plaice (*Pleuronectes platessa*), in Galway Bay, on the west coast of Ireland. Monthly surveys were carried out in the period after peak settlement over two years. Variability in flatfish density and Fulton's K condition was explained in relation to biotic and abiotic habitat characteristics, differing within and between distinct nursery grounds. Dab were concentrated in deeper waters, were negatively associated with shrimp densities and salinity and their abundance showed a decrease from June to September combined with interannual variation. Plaice densities were highly associated with shallower depths and high polychaete and shrimp densities and were negatively related with increased macroalgal cover and organic content. Most of the variability in Fulton's condition was explained by the same set of variables for both species; year and densities of crab and malacostracans. This analysis revealed important ecological mechanisms allowing the co-existence of two flatfish species in nursery grounds. However, high quality nursery grounds for dab and plaice differed and anthropogenic and climatic impacts on flatfish nurseries are likely to have a different impact on plaice and dab populations. Knowledge gained about the quality of nursery habitat for commercially important fish species provides a basis for mapping essential flatfish habitats to inform management plans for coastal areas.

1. Introduction

Nursery grounds for many flatfish species, including plaice (*Pleuronectes platessa*) and dab (*Limanda limanda*), are located in shallow soft-bottom coastal areas (Norcross et al., 1995). Both the quantity and quality of these habitats are important factors that regulate annual levels of recruitment to the adult stocks in offshore waters (Gibson, 1994; Rijnsdorp et al., 1992). Habitat selection by juvenile flatfish is driven by resource requirements promoting fast growth and survival during this vulnerable life stage (Gibson, 1994). Individual species are restricted to a range of habitat conditions by physiological tolerances (Davenport and Sayer, 1993), feeding requirements (Piet et al., 1998), sediment associations (Moles and Norcross, 1995) or vulnerability to predators (Ryer et al., 2008) and this may lead to spatial segregation or overlap between species. Fundamental knowledge of habitat characteristics directly affecting the distribution and growth of juvenile fish is crucial to support decision making for the protection and management of nursery areas (Maxwell et al., 2009).

The need for a successful approach to assessing essential habitat for juvenile fishes has lead to the development of habitat suitability models. These models use a measure of fish abundance (e.g. presence absence, counts, densities) as a response variable to relate their distribution to a set of environmental factors. The physical variables: depth, substratum and temperature have been identified as the strongest indicators of fish occurrence for numerous flatfish species over large spatial scales (Able et al., 2005; Abookire and Norcross, 1998; Florin et al., 2009; Norcross et al., 1995). The integration into these models of biological elements of the habitat, including prey and predator abundances, allows for a more complete assessment of nursery quality (Le Pape et al., 2007; Nicolas et al., 2007; Vinagre et al., 2006; Wennhage et al., 2007). Studies on small-scale variability in the habitat use of juvenile fish within nursery areas are less common but can gain additional insight into the response of a population to environmental gradients (Allen and Baltz, 1997; Maes et al., 2004). This is particularly important since the same environmental variables may not always explain habitat use at different spatial scales. On the one hand, it has been shown that different habitat features explained variability in fish density between a whole estuary and a type of favored habitat within that estuary (Nicolas et al., 2007); or between all estuaries along the coast and the individual estuaries (Vasconcelos et al., 2010). On the other hand, large-scale models developed for estuaries or coastal areas (Cabral and Costa, 1999; Le Pape et al., 2003) were successfully adapted to individual estuaries or sites within estuaries (Nicolas et al., 2007; Vinagre et al., 2009). Therefore, studies investigating small-scale variability in

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* Corresponding author. Tel.: +353 91742502.
E-mail address: fienderaedemaecker@yahoo.com (F. De Raedemaecker).

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habitat use will add understanding on the ecological processes in nursery grounds and may contribute to the development of habitat suitability modeling of these species at larger scales.

Most studies on the quality of nursery habitat and its effect on recruitment variability for different flatfish species are based on density measures (Le Pape et al., 2003; Vasconcelos et al., 2010). Areas occupied at the highest densities may represent the best available habitat and should be indicative of the species' requirements (McConnaughey and Smith, 2000). Likewise, an uneven distribution within the area of occurrence may indicate small-scale differences in habitat quality. However, recruitment to the adult stock does not only depend on the numbers of juveniles that reach nursery areas (Beck et al., 2001). Other (density dependent) mechanisms affecting juvenile fish are known to dampen the variability generated in the larval period (Houde, 2008; Myers and Cadigan, 1993; Nash and Geffen, 2000). Houde (1989) showed that cohorts of fast-growing fish that reach a large size early in life experience lower cumulative, stage-specific mortality and have a higher probability to recruit. Measures of growth rate and condition of juvenile fishes may therefore reflect the probability of survival and can be used as indicators of habitat quality (Amara et al., 2009; Vasconcelos et al., 2009).

Despite the growing body of literature describing early life history parameters of flatfish, there is limited information on the combined effect of physical and biological habitat characteristics that influence small-scale differences in the distribution and growth of plaice and dab. A mechanistic understanding of the association between habitat features and growth of juvenile fish is crucial to evaluate anthropogenic and climatic impacts on flatfish nurseries and ultimately fish stocks. The objective of the present work was to assess the quality of flatfish nursery grounds in Galway Bay, on the west coast of Ireland, using data on the density and Fulton's K condition of juvenile fish in relation to a set of abiotic and biotic habitat characteristics. Sampling surveys during two years and covering the months after peak abundance were carried out within four distinct nurseries. The first aim was to determine small-scale spatial and temporal variation in density and Fulton's K condition for both species and to identify nurseries in Galway Bay that represent habitat of relatively high quality for juvenile plaice and dab. The second aim was to ascertain a set of habitat characteristics explaining small-scale variability in density and Fulton's K condition of juvenile plaice and dab.

2. Materials and methods

2.1. Study area and sampling strategy

The westward facing Galway Bay is a region of high tidal energy (tidal range of 4.5 m), with an area of c. 100 km^2, located on the west coast of Ireland (Fig. 1). A total of four soft-bottom nursery areas which were isolated from each other by rocky shorelines were selected from within the inner Galway Bay for sampling. Ballyloughaun and Silverstrand are two small embayments in the northern section which receive a considerable freshwater input by the Corrib River. Ballyvaughan and Traught are located in the southern section of Galway Bay; the former is characterized by a substantial intertidal area whereas the latter is a small beach, located on a straight, mainly rocky coastline.

Juvenile flatfish assemblages were sampled monthly from June to September in 2008 and 2009. Due to weather conditions in June 2008, sampling was only undertaken in Ballyloughaun that month and the three other nursery areas were surveyed three weeks later in July 2008, whereas no sampling was undertaken in Ballyloughaun in July 2008. A 1.2 m beam trawl (6×6 mm codend) equipped with one tickler chain was hauled by a small dinghy at a constant velocity of 1.1 knots (34 m/min) for 2 min. This speed was chosen since it gave the largest catches of 0-group plaice using a two-meter beam trawl in Loch Ewe (Edwards and Steele, 1968; Riley and Corlett, 1966). The beam trawl was hauled parallel to the shore to cover an area with a homogeneous depth. Tidal height for every haul was calculated using tide tables for Galway Bay and the exact time of hauling. The actual depth was recorded with an echo sounder and used in combination with tidal height to obtain the depth relative to lowest astronomical tide (depth LAT; expressed as 'negative depths' when working over the intertidal area) and the depth zone (intertidal or subtidal) for every haul. Three

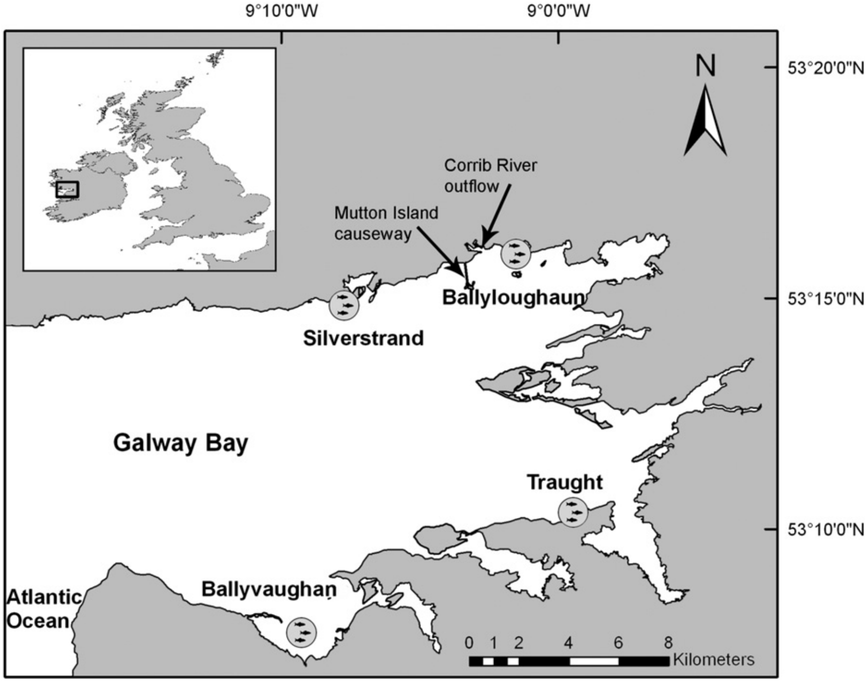

Fig. 1. Map of Galway Bay, Ireland, showing the position of four sampled flatfish nursery grounds.

replicate trawl hauls were carried out both intertidally and subtidally, resulting in a total of six hauls at each site. A mechanical flowmeter attached to the beam was used to calculate the distance towed and ultimately the swept area, which averaged 94.2 ± 16.8 m^2 per trawl. The geographic location of the trawls was recorded using a GPS and bottom salinity and bottom temperature data were obtained at each trawl location with a CTD.

All juvenile flatfish were immediately stored onboard in liquid nitrogen and transferred to a −80 °C freezer in the laboratory until further sorting and analyses. Shore crab (*Carcinus maenas*) and brown shrimp (*Crangon crangon*) were the most abundant predators during spring and summer in Galway Bay and all hauled specimens were counted and measured before releasing them, simultaneously with the few other occurring species of shrimp (e.g. *Palaemon serratus*) and crab (e.g. *Necora puber*). Only crab and shrimps >3 cm were assessed since laboratory experiments carried out by van der Veer and Bergman (1987) determined this to be the minimum size enabling predation on 0-group plaice. The amount of macroalgae in each trawl was used to obtain a relative measure of the abundance of macroalgae on the seabed, using a qualitative scale ranging from 0 (no macroalgal cover) to 5 (filling a bucket of 50 l). Macrobenthos at each end of the trawl path were collected from three replicate Van Veen grabs (0.025 m^2) pooled together. A fourth grab was collected for the determination of sediment organic matter and particle size analysis.

2.2. Fish processing

All fish were counted and identified to determine the densities (individuals 100 m^{-2}) of the different species of 0-group flatfish in each trawl. Standard length of freshly thawed and gently blotted fish were measured to the nearest mm and weighed to the nearest mg. Fulton's K condition factor was calculated for each fish using the formula $K = (W/L_s^3) * 100$, where W is freeze-thawed wet weight (g) and L_s is standard length (cm). Standard length and not total length was used in this formula since some caudal fins were partly lost during beam trawling. This should be taken into account when comparing the Fulton‘s K condition values obtained here with other studies. Classification of age-0 and age-1+ flatfish was carried out by identifying and counting the opaque zones on the sagittal otoliths using a stereomicroscope.

2.3. Sediment processing

All sediment samples collected for macrobenthos determination were washed on a 1 mm sieve and stored in 4% buffered formaldehyde prior to counting and identifying to class level using a stereomicroscope. The main prey items of plaice and dab (polychaetes, bivalves and malacostracans) were counted and the three grabs from either side of the haul were pooled before calculating the density of the different prey taxa and the total prey density per 100 m^{-2} representing a trawl haul. Organic matter was measured using the percentage loss on ignition (LOI) after burning 25 g of sediment (oven-dried at 100 °C to constant weight) in a muffle furnace at 450 °C for 6 h (Bale and Kenny, 2007). Particle size analysis was carried out with oven-dried sediment for all samples collected in 2008 using the method described in Bale and Kenny (2007). Sediments were divided into six fractions: silt (<63 μm diameter), very fine sand (63 μm–125 μm), fine sand (125 μm–250 μm), medium sand (250 μm–500 μm), coarse sand (500 μm–1 mm) and gravel (>1 mm). Each fraction was weighed, expressed as a percentage of the total weight and the mean sediment particle size, phi (φ), was calculated. The sediment particle size data was mapped with ArcGIS 9.2 software as continuous surfaces using inverse-distance weighted averaging (IDW). This interpolation technique was applied to generate % composition data at the sample locations in 2009, as it proved effective in other studies (Compton et al., 2008; Phelan et al., 2001; Stoner et al., 2001). Samples from either side of the trawl haul were analyzed separately and mean values of organic matter and mean particle size per trawl were calculated.

2.4. Data analyses

The R environment (R Development Core Team, 2008) was used to investigate variability in density (by generalized linear modeling (GLM)) and condition (by generalized linear mixed modeling (GLMM)) of plaice and dab. Different modeling methods for density and condition were applied due to their differential numbers of observations per haul. Only one density figure corresponded per haul whereas a higher and uneven number of observations of condition were obtained per haul and a random haul effect was therefore included in the GLMMs to account for correlations between observations per hauls. Modeling the variation in dab density was carried out in two steps due to the high proportion of zero catches: a logistic regression model with a logit link was first fitted to estimate the probability of presence and a Gaussian regression model was second fitted to account for the variability in (log-transformed) densities conditional to positive catches (Le Pape et al., 2007). The last model was compared with a Gamma regression model with a log link but the Gaussian regression model had a consistent better model validation. Although some authors have suggested that the use of gamma density is preferable to the use of a lognormal density for fisheries data (Myers and Pepin, 1990), others have argued that both analyses will usually produce similar results (McCullagh and Nelder, 1989).

The two species were analyzed separately, as were the data for density and condition. Initially, a first set of models investigated differences in density and condition for each species in relation to nursery ground and time of sampling (including the interactions of year with ordinal date and with nursery ground to explore interannual consistency). Since flatfish densities and condition may not necessarily change in a linear fashion over time, a quadratic and cubic function of time was introduced in the model fits.

With a second set of models, habitat characteristics accounting for small-scale variability in condition and density of plaice and dab were identified. Prior to analysis, data were tested for outliers, normality and homogeneity of variances and log transformations were carried out if required (Zuur et al., 2009). Data were pair-plotted in order to investigate and eliminate multi-colinearity between independent variables. Following this preliminary analysis, the variables considered in the models described characteristics of prey (density of polychaetes, malacostracans), predators (density of crab and shrimps), competitors (density of plaice and dab), substrate (organic content, macroalgal coverage and mean sediment particle size (although not considered in the dab models due to co-linearity with density of malacostracans)), other abiotic variables (bottom salinity, bottom temperature, actual depth and depth LAT (depth zone was used instead in the ‘Dab presence/absence’ model due to higher explanatory power)) and time (year and ordinal date). A backwards selection using the Akaike Information Criterion (AIC) was used for model selection, followed by a systematic removal of variables based on a significance level of 0.05. Model validation was always carried out by plotting model residuals against the explanatory variables and by creating partial regression plots. The goodness-of-fit of the predictors was assessed by comparing their relative contribution to the total deviance explained. After obtaining the optimal models, the predictor ‘site’ was added to investigate if this improved the optimal model, suggesting that other variables not measured in this study contributed to variation between nursery grounds, or if it replaced some of the habitat features, suggesting that these did not attribute to within-site variability but explained differences between nursery grounds. All predictor variables were continuous except for year, site, depth zone and macroalgal coverage which were included as categorical variables.

3. Results

3.1. Spatial and temporal patterns of juvenile flatfish assemblage in Galway Bay

From the content of 72 trawls in 2008 and 96 trawls in 2009, a total of 653 (2008) and 921 (2009) age-0 flatfish plus 12 (2008) and 56 (2009) age-1+ flatfish were sampled. Six flatfish species were identified. Common sole (*Solea solea*), turbot (*Psetta maxima*), European flounder (*Platichthys flesus*) and brill (*Scopthalmus rhombus*) were not further analyzed due to their low occurrence over all sampling events (<2% of all age-0 flatfish). Plaice (*P. platessa*) were the most numerous overall, representing 83% of age-0 catch, and dab (*L. limanda*) accounted for 15% of age-0 catch. Plaice occurred in 96% of all trawls whereas the occurrence of dab was 10% and 74% in the intertidal and subtidal zone respectively. Averaged over both years, we recorded a mean density of 8.2 100 m^{-2} for plaice and 2.6 100 m^{-2} for dab in the subtidal area. Unimodal length–frequency distributions showed that plaice and dab did not settle after June but length ranges of dab in June were generally smaller than those of plaice and plaice attained a longer length at the end of the summer (Fig. 2). Table 1 summarizes the average fish and habitat measurements per nursery area and year.

3.2. Spatial and temporal variability in density and Fulton's K condition

Table 2 shows the effect of site, year and ordinal date on the density/presence and Fulton's condition index of plaice and dab. The probability of encountering dab did not differ between sites, years or months and a spatial or temporal trend was absent in both years. Dab densities did not differ between sites but were consistently higher in 2008 than in 2009 in all sites and showed a consistent decrease within a year. Plaice densities did not differ between or within years but were consistently higher in Ballyloughaun and Traught compared to Ballyvaughan and Silverstrand in both years. Mean values of Fulton's K condition for dab and plaice were higher in 2009 than in 2008 and within years the condition was variable over time, as indicated by the interaction term on year and third order of ordinal date (Figs. 3 and 4). For both species there was a significant site effect; dab were in better condition in Ballyvaughan and Silverstrand whereas plaice were in better condition in Ballyloughaun and Silverstrand; this was consistent over the two years.

3.3. Habitat characteristics explaining variability in density

Small-scale variability within nursery grounds was found in dab presence and density based on habitat characteristics, explaining 35% and 39% of the optimal model (Table 3 and Fig. 5a). Most of the variability in the probability of encountering dab was predicted by depth; with dab more likely to occur in the subtidal area. Ordinal date was the second most important explanatory variable; the probability of encountering dab increased with time. The addition of site significantly improved this optimal model indicating that other variables not measured in this study contributed to variation in dab distribution between nursery grounds.

Small-scale variability in dab densities (Table 3 and Fig. 5b) were mainly driven by ordinal date, with numbers decreasing from June to September. Depth was the second most important variable for predicting dab densities, with higher numbers occurring in deeper waters. Densities were higher in 2008 and decreased with increasing numbers of shrimps and with increasing salinity. Site was not significant in this optimal model indicating that habitat features driving small-scale differences in dab densities were similar across the sampled sites.

In contrast to dab, small-scale variation in plaice distribution is more unpredictable, as suggested by the optimal model which only explained 19% of the total variability in plaice density (Table 3 and Fig. 5c). In contrast to dab densities which were more associated with actual depth, variability in plaice density was best described by the depth relative to the lowest astronomical tide, with lower plaice densities found in subtidal areas. The density of shrimps was the second most important variable in the model, with high numbers of this predator associated with high numbers of plaice. Plaice density was also found to increase with polychaete density and to decrease with algal cover and organic content. However, the organic content, polychaete and shrimp densities explained overall differences in plaice densities between sites and did not contribute to small-scale variability within sites. In this respect, only depth and macroalgal cover

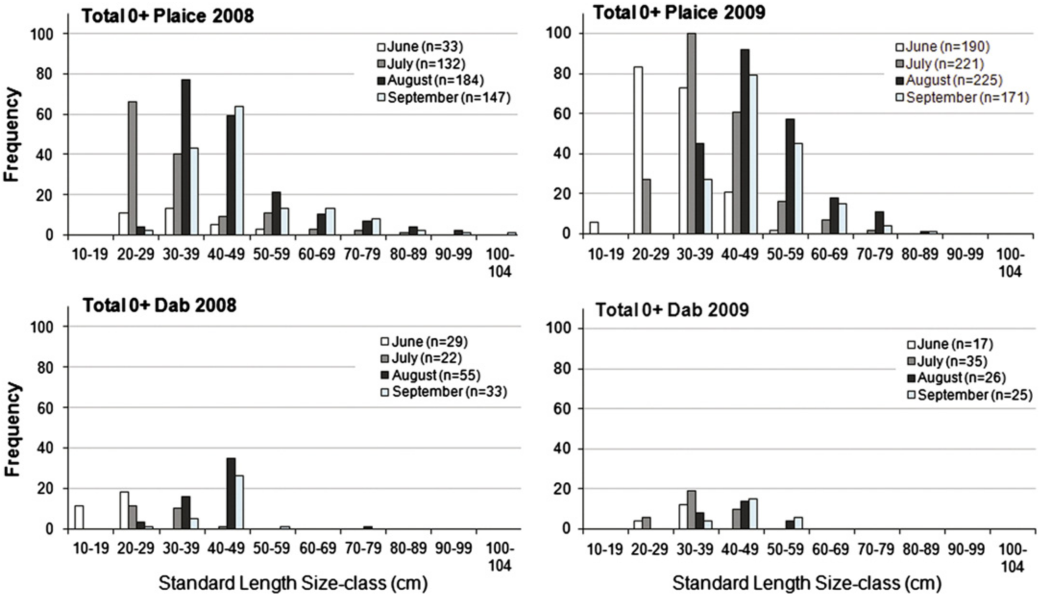

Fig. 2. Monthly length–frequency distributions of 0-group plaice and dab pooled over all sites and presented per sampling year. Total sampled fish numbers per month are presented in parentheses.

proved to explain variability in plaice density over larger spatial scales between distinct nursery areas within Galway Bay.

3.4. Habitat characteristics explaining variability in Fulton's K condition

Habitat characteristics attributed to small-scale condition differences of plaice and dab (Table 4 and Fig. 6). Lower flatfish condition was associated with high numbers of crab. High densities of malacostracans were associated with a low plaice condition and a high dab condition. Variability in plaice condition was explained by the previous three predictors only, while dab condition also increased with decreasing depth and organic content (which is positively co-linear with particle size in the dataset of dab condition) and with increasing polychaete densities. Densities of potentially competitors (other flatfish species) had no effect on plaice or dab condition. The factor site did not reduce the residual deviance of the optimal model and thus did not contribute to any additional variability in dab and plaice condition. The optimal model predicting the variability in dab condition is more complete (73%) than the one for plaice condition (47%).

4. Discussion

Density and Fulton's K condition of plaice (*P. platessa*) and dab (*L. limanda*) in Galway Bay varied spatially and temporally and was influenced by a variety of habitat characteristics. Dab occurrence was only associated with depth and ordinal date whereas dab and plaice densities were related to a combination of physical and biological variables. Juvenile condition was mainly predicted by biological variables, with depth and organic content explaining additional variability in plaice condition. The explained variability in density and condition was greater for dab than for plaice, possibly due to the larger sample size or distribution range of plaice. The percentage of density variability explained by habitat characteristics was similar to those reported in other studies, which often range around 20% and seldom exceed 50% (Le Pape et al., 2003, 2007; Vasconcelos et al., 2010). The nature of juvenile flatfish distribution is generally very patchy (Modin and Pihl, 1996) and it is known that physical descriptors do not always account for its variation (Le Pape et al., 2003), causing much of the remaining unexplained variability in the density models. In contrast, the explained variability in juvenile condition was higher, reaching > 70% for dab. This might reflect that fish condition is influenced by differences in habitat conditions which we have more precisely quantified than other, likely complex, factors that cause fluctuations in fish densities. Additionally, more observations of fish condition compared to fish density per haul and the resulting difference in modeling procedure (GLMM vs. GLM) may add to the differences in residual deviance.

4.1. Temporal variability in density and condition

This study recorded interannual variability in the density of 0-group dab, in the condition of dab and plaice and in the fish length of both species just after settlement. It is generally accepted that year-class strength varies greatly between years due to fluctuating environmental conditions during egg and larval development (Beggs and Nash, 2007; Beverton and Iles, 1992; Gibson, 1994; van der Veer et al., 2000). A more favorable environment during the larval phase in 2009 may have resulted in the consistently higher fish condition and average fish length just after settlement. Winter and spring temperatures, as recorded from the M1 buoy outside Galway Bay, were on average 1 °C lower in 2009 than in 2008 (Marine Institute, pers. comm.) and may have contributed to the higher fish condition observed in 2009. This would be in accordance with other studies reporting a negative correlation between spring seawater temperature and year-class strength of many flatfish species (Haynes et al., 2010; Henderson, 1998; Henderson and Seaby, 1994; Pihl, 1990; van der Veer, 1986). However, a more comprehensive analysis

Table 1
Overall ranges and averages ± SE of fish and habitat characteristics presented per nursery ground and year and averaged over all sites per year.

	Ballyloughaun		Ballyvaughan		Silverstrand		Traught		Average		Overall range
	2008	2009	2008	2009	2008	2009	2008	2009	2008	2009	
Plaice density (100 m^{-2})	8.6 ± 1.8	11.3 ± 1.7	6.2 ± 1.6	7.9 ± 1.4	5.2 ± 1.2	4.1 ± 0.6	9.8 ± 1.9	12.0 ± 1.8	7.4 ± 0.8	8.8 ± 0.8	0–29.6
Dab density subtidally (100 m^{-2})	5.6 ± 1.6	1.8 ± 0.5	0.9 ± 0.3	1.9 ± 0.6	2.7 ± 0.7	2.3 ± 0.6	4.9 ± 1.2	1.6 ± 0.5	3.5 ± 0.6	1.9 ± 0.3	0–16.3
Plaice condition (g cm^{-3})	1.74 ± 0.03	1.95 ± 0.02	1.73 ± 0.03	1.92 ± 0.02	1.81 ± 0.03	1.99 ± 0.03	1.70 ± 0.02	1.90 ± 0.02	1.75 ± 0.01	1.94 ± 0.01	1.34–2.45
Dab condition (g cm^{-3})	1.56 ± 0.06	1.79 ± 0.03	1.73 ± 0.06	1.94 ± 0.06	1.76 ± 0.05	1.88 ± 0.04	1.66 ± 0.02	1.89 ± 0.05	1.66 ± 0.03	1.87 ± 0.03	1.25–2.24
Bottom salinity	30.2 ± 0.8	27.6 ± 1.1	32.0 ± 0.2	33.1 ± 0.1	26.8 ± 0.8	29.9 ± 0.7	32.0 ± 0.1	31.8 ± 0.5	30.3 ± 0.4	30.6 ± 0.4	12.1–34.6
Bottom temperature (°C)	15.9 ± 0.2	17.5 ± 1.0	15.5 ± 0.2	15.4 ± 0.3	15.9 ± 0.2	15.6 ± 0.4	16.3 ± 0.3	16.3 ± 0.4	15.9 ± 0.1	16.2 ± 0.3	12.4–28.0
Crab density (100 m^{-2})	5.8 ± 1.2	6.5 ± 0.9	11.0 ± 2.0	14.5 ± 1.8	2.6 ± 0.5	2.8 ± 0.5	7.1 ± .1.0	11.0 ± 1.7	6.6 ± 0.7	8.7 ± 0.8	0–41
Shrimp density (100 m^{-2})	16.1 ± 3.4	4.0 ± 1.1	28.7 ± 8.3	16.0 ± 4.6	20.0 ± 5.7	7.8 ± 1.4	20.9 ± 3.6	20.0 ± 3.3	21.4 ± 2.8	12.0 ± 1.6	0–100
Organic content (%)	1.14 ± 0.10	0.95 ± 0.08	1.12 ± 0.07	0.86 ± 0.05	0.98 ± 0.03	0.90 ± 0.02	0.91 ± 0.04	0.64 ± 0.03	1.04 ± 0.03	0.84 ± 0.03	0.36–1.77
Mean particle size (ϕ)	3.26 ± 0.08	3.34 ± 0.06	2.66 ± 0.09	2.53 ± 0.07	2.97 ± 0.06	2.90 ± 0.04	2.33 ± 0.04	2.23 ± 0.05	2.81 ± 0.05	2.75 ± 0.05	1.71–3.78
Polychaete density (m^{-2})	98.9 ± 12.0	137.9 ± 13.6	115.6 ± 27.6	149.4 ± 22.3	66.7 ± 15.3	46.9 ± 7.5	57.4 ± 10.5	82.5 ± 8.9	84.6 ± 9.1	104.2 ± 8.2	0–500
Bivalve density (m^{-2})	9.6 ± 2.1	27.4 ± 5.9	112.2 ± 23.4	209.6 ± 22.4	175.9 ± 21.5	171.8 ± 18.3	295.6 ± 46.5	580.4 ± 57.5	148.3 ± 18.5	247.3 ± 26.3	0–1230
Malacostracan density (m^{-2})	4.1 ± 1.4	4.9 ± 1.7	51.1 ± 12.8	187.1 ± 50.3	31.9 ± 5.7	86.4 ± 14.5	112.2 ± 17.1	167.5 ± 20.5	49.8 ± 7.2	111.5 ± 153.7	0–1110
Total prey density (m^{-2})	120 ± 16	172 ± 17	323 ± 43	569 ± 62	292 ± 39	322 ± 31	487 ± 54	865 ± 63	305 ± 25	482 ± 36	27–1600

Table 2
Predictors explaining spatial and temporal variability in presence absence and/or density (using generalized linear modeling (GLM)) and Fulton's K condition (using generalized linear mixed modeling (GLMM)) of dab and plaice. Columns indicate residual degrees of freedom (DoF) and residual deviance of the model for each added variable. The 1st order linearity corresponds to a linear relationship and a 3rd order to a cubic relationship in ordinal date. Results of pairwise tests are shown between brackets (Bl: Ballyloughaun, Bv: Ballyvaughan, Si: Silverstrand, Tr: Traught). NS = non-significant at a 5% level.

	Dab presence/absence		Dab density		Plaice density		Dab condition		Plaice condition	
	DoF	Residual deviance	DoF	Residual deviance	DoF	Residual deviance	DoF	Residual deviance	DoF	Residual deviance
NULL	167	228.86	70	3.82	167	22.28	221	8.80	1252	4.76
Site		NS		NS	164 (Bl,Tr > Bv,Si)	20.19	218 (Bv,Si > Bl,Tr)	6.81	1249 (Bl,Si > Bv,Tr)	39.99
Year		NS	69	3.65		NS	217 (2009 > 2008)	4.66	1248 (2009 > 2008)	29.60
Ordinal date		NS	68	3.10 1st order		NS	214 1st order	3.56	1245 3rd order	28.37
Ordinal date :Year		NS		NS		NS	211 3rd order	3.05	1242 3rd order	27.18
Site: year		NS		NS		NS		NS		NS

of the temperature experienced by these fish during the larval phase and a longer time series would be needed to confirm this link.

Temporal fluctuations in flatfish densities in Galway Bay showed interspecific differences. Dab densities declined from June to September while the probability of dab occurring in the trawls increased during the same period. It is possible that the dab distribution becomes less patchy as they grow older and become more active foragers. Strong site-fidelity of juvenile plaice has previously been observed in tagging experiments (Burrows et al., 2004) but more experimental studies are needed to establish the dispersal rates with age or time for various flatfish species. Reported peaks in the timing of dab settlement vary widely between habitats, with densities reaching a maximum between June and October (Amara, 2004; Amara et al., 2001; Beggs and Nash, 2007; Bolle et al., 1994; Poxton et al., 1982). Plaice densities in Galway Bay did not show fluctuations between or within years contrasting with results from previous studies, which show highest densities between April and July and a subsequent population decline (Amara and Paul, 2003; Freitas et al., 2010; Hjörleifsson and Pálsson, 2001; Modin and Pihl, 1994; Nash and Geffen, 2000; Pihl et al., 2000; Poxton et al., 1982; van der Veer et al., 1990). In contrast, a population decline for dab in Galway Bay was detected in this study. Similar results were reported in the Clyde Sea area where interspecific differences in timing of fish emigration from nursery areas were proposed to account for this variation (Poxton et al., 1982). Earlier settlement and faster growth of plaice compared to dab was revealed from monthly length–frequency distributions and may reflect temporal resource partitioning, which is a strategy used by morphologically similar species to reduce interspecific competition (Schoener, 1974).

4.2. Environmental variables explaining variability in density and condition

Habitat use of plaice and dab in nursery areas in Galway Bay appeared to be primarily influenced by depth. Settled plaice were restricted to shallow water with peak densities occurring around 1 m. This is consistent with other studies which rarely report plaice in depths > 3 m (Poxton et al., 1982) and which show that plaice display a tidal rhythm, moving closer to the beach at high tide (De Veen, 1978; Gibson, 1973). Depth distributions of settling dab have not been previously studied on the west coast of Ireland and an increase in dab density was recorded with depth. Our sampling efforts were restricted to 5 m depth but it is likely that settlement also occurs in

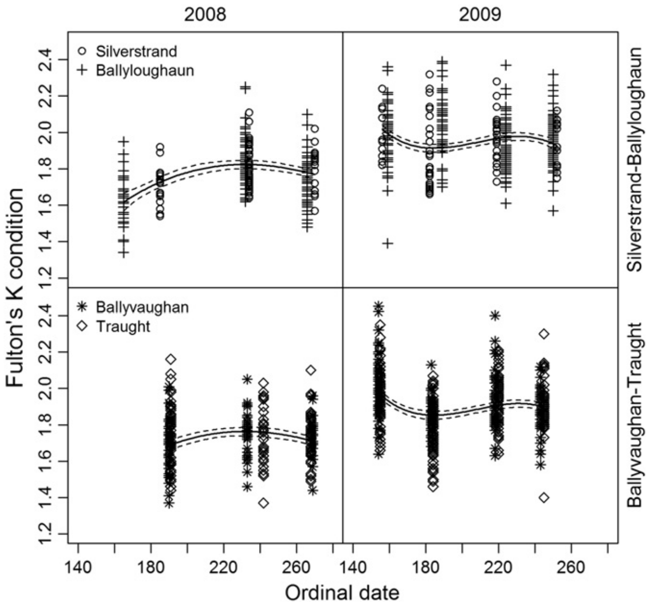

Fig. 3. Fulton's K condition of plaice collected in four different nursery grounds between June and September in two years. Each dot represents a fish and the fitted lines with 95% confidence intervals are the mean predicted values from a GLMM with predictors; site, year, ordinal date (cubic relationship) and the interaction between year and ordinal date (as described in Table 1).

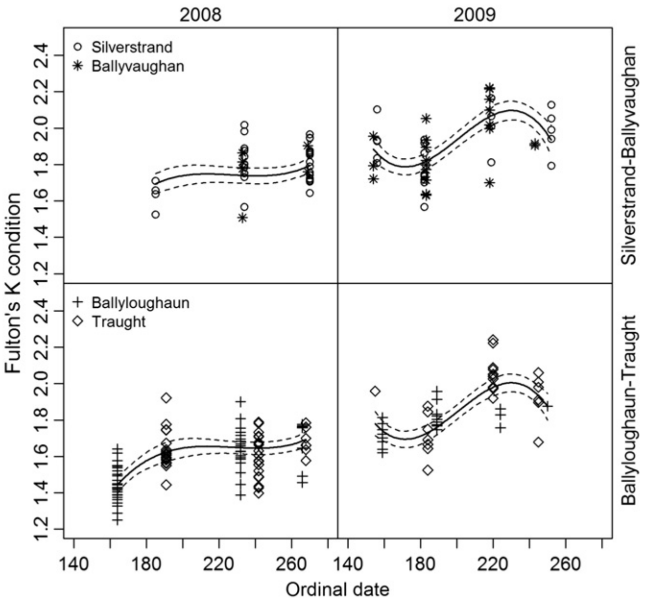

Fig. 4. Fulton's K condition of dab collected in four different nursery grounds between June and September in two years. Each dot represents a fish and the fitted lines with 95% confidence intervals are the mean predicted values from a GLMM with predictors; site, year, ordinal date (cubic relationship) and the interaction between year and ordinal date (as described in Table 1).

Table 3

Goodness-of-fit statistics for the GLMs fitted to predictors of small-scale variability in the presence absence and/or density of dab and plaice. Predictors are ordered with increasing explanatory power based on AIC values when comparing the information loss after every predictor is alternatively removed from the optimal model. Residual degrees of freedom (DoF), residual deviance of the model for each added variable and the percentage of the total deviance explained are indicated in the columns. Variables shaded in grey become insignificant upon addition of 'site' in the optimal model.

	Parameters		Estimate	Std. error	z value	p	DoF	Residual deviance	% Expl
Dab presence/absence									
NULL							167	228.86	
	Intercept		−5.065	1.348	−3.758	<0.001			
	Ordinal date		0.013	0.006	2.336	0.0195	166	225.48	
	Depth	Subtidal	3.313	0.457	7.247	<0.001	165	14.03	
RESIDUAL									35.32
Dab density (log)									
NULL							70	3.82	
	Intercept		1.953	0.367	5.325	<0.001			
	Salinity		−0.019	0.009	−2.125	0.0374	69	3.81	
	Shrimp density (log)		−0.140	0.579	−2.424	0.0181	68	3.80	
	Year	2009	−0.169	0.054	−3.133	0.0026	67	3.57	
	Actual depth		0.097	0.024	4.014	<0.001	66	3.21	
	Ordinal date		−0.004	0.001	−4.984	<0.001	65	2.33	
RESIDUAL									38.94
Plaice density (log)									
NULL							167	22.88	
	Intercept		0.581	0.179	3.249	0.0014			
	Organic content		−0.210	0.093	−2.270	0.0246	166	21.29	
	Weed		−0.050	0.020	−2.460	0.0149	165	20.00	
	Polychaete density (log)		0.198	0.074	2.689	0.0079	164	20.05	
	Shrimp density (log)		0.149	0.053	2.835	0.0052	163	19.36	
	Depth LAT		−0.102	0.028	−3.593	<0.001	162	18.53	
RESIDUAL									19.03

deeper waters, as reported in offshore waters in the North Sea and Irish Sea with peak densities within 10 m but settlement extending up to 70 m depth (Beggs and Nash, 2007; Bolle et al., 1994; Dickey-Collas et al., 1997). The rare appearance of dab in intertidal areas in Galway Bay supports the absence of a tidal transport pattern for this species. This spatial segregation between plaice and dab in Galway Bay may add to the temporal resource partitioning resulting in a reduction of interspecific competition between plaice and dab.

Salinity is an important determinant of flatfish community structure (Schreiber, 2001) and has a larger effect on juveniles of marine migrants inhabiting estuaries like flounder and Senegalese sole (*Solea senegalensis*) (Cabral et al., 2007; Franco et al., 2008; Ramos et al., 2009). To a lesser extent it also affects distribution and growth patterns of flatfish in coastal zones due to differences in osmoregulatory capacity (Lyndon, 1994). Dab densities were slightly higher in less saline areas in Galway Bay, but a response to salinity was not reflected in plaice densities or flatfish condition. The higher dab density in less saline areas is in accordance with similar findings for plaice in the Humber estuary where younger fish used lower salinity areas to enhance growth (Marshall and Elliott, 1998). The influence of salinity on juvenile growth depends on the developmental stage (Jager et al., 1993) and this might be the reason that salinity did not explain overall variability in dab and plaice condition in Galway Bay.

Although temperature is known to be an important environmental determinant of juvenile distribution and growth (Fonds et al., 1992; Reichert et al., 2000; Yamashita et al., 2001), no direct link with flatfish density or condition was detected in this study. It is possible that fish condition was not affected by the temperature at the time of the survey, but by that in the preceding period. Alternatively, the moderating effect of temperature may have partly been expressed by time, water depth or prey and predator abundance in the resulting models. Temperature loggers at a finer temporal scale should have been used to reveal possible site differences.

The present study revealed the influence of substrate characteristics (particle size, prey abundance and organic content) on the density and condition of juvenile flatfish. It is well known that sediment structure co-varies with other, especially prey related, substrate characteristics (Gibson, 1994; McConnaughey and Smith, 2000), which was also observed in Galway Bay. The condition of dab was positively associated with particle size demonstrating the negative effect of muddy locations with consequently lower prey density. Sediment properties may directly enhance survival of demersal fish by permitting burying behavior critical for conserving energy by reducing metabolic rates (Howell and Canario, 1987) or for escape from predators (Gibson and Robb, 1992; Jager et al., 1993; Stoner and Abookire, 2002). The absence of a relationship between plaice condition and sediment particle size suggests a wider tolerance of plaice to varying sediment substratum. Burial behavior studies showed that newly metamorphosed plaice are unable to bury in grain sizes larger than 500 μm (Riley et al., 1981) and avoid sediment with more than 10% mud fraction (Jager et al., 1993); average grain size in the studied nurseries in Galway Bay was generally within those extremes. Sediment properties in Galway Bay had an additional impact on flatfish condition through the composition and abundance of benthic invertebrates. High polychaete and malacostracan densities were associated with high dab condition whereas plaice condition was negatively correlated with malacostracan density. This highlights the different feeding strategies of plaice and dab, with a higher constitution of malacostracans in dab diet as described by previous dietary analysis of juveniles in Galway Bay (De Raedemaecker et al., 2011a). This study showed that availability of favorable macrobenthic prey is crucial for rapid growth of flatfish and its effect might possibly exceed that of sediment particle size. This is also suggested by previous laboratory experiments indicating the complexity of interrelated factors in habitat choice (Phelan et al., 2001).

The negative correlation of organic enrichment with plaice density and dab condition is most likely indicative of the deteriorated feeding

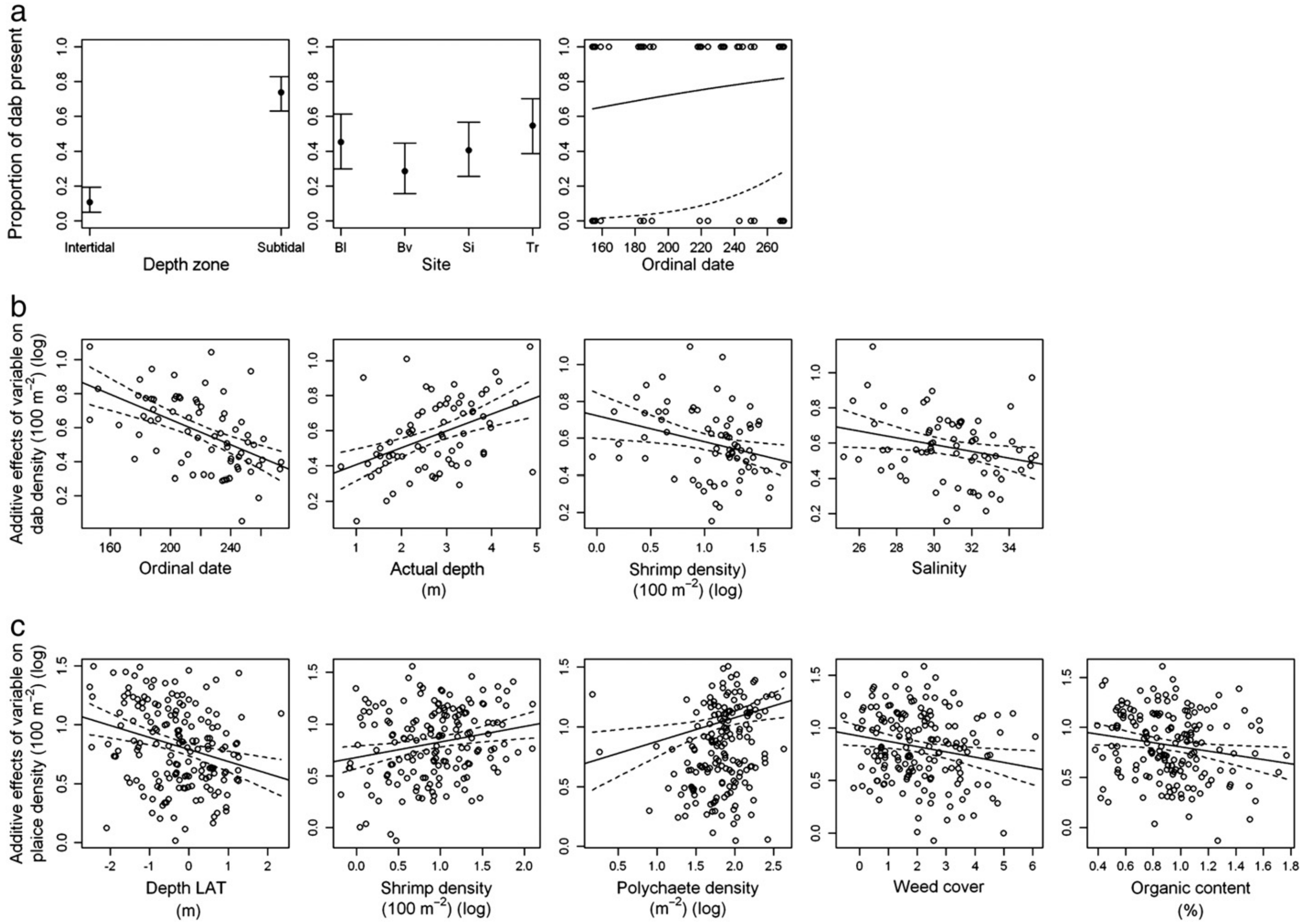

Fig. 5. (a) Proportion of dab presence and absence in a total of 168 trawl hauls over four sites and between June and September in two years, separated by depth stratum, site (using the Clopper–Pearson method) and by sampling time throughout the post-settlement period (using a binomial GLM with dashed line: intertidal area, solid line: subtidal area), (b) GLM plots showing additive effect of each significant variable on positive dab densities per haul (n = 71) over four sites and two years, (c) GLM plots showing additive effect of each significant variable on plaice densities (n = 162) over four sites and two years.

circumstances associated with organic content, which generally provides information on productivity of meio- and macro-faunal invertebrates in nursery grounds (Möller et al., 1985). With low organic matter, invertebrate biomass will likely increase whereas higher values of organic matter can lead to high levels of oxygen consumption and subsequent anoxia and elimination of macrobenthos (Pearson and

Table 4
Goodness-of-fit statistics for the GLMMs fitted to predictors of small-scale variability in Fulton's K condition of dab and plaice. Predictors are ordered with increasing explanatory power based on AIC values when comparing the information loss after every predictor is alternatively removed from the optimal model. Residual degrees of freedom (DoF), residual deviance of the model for each added variable and the percentage of the total deviance explained are indicated in the columns. The mean sediment particle size was correlated with the abundance of malacostracans, bivalves and total prey (−0.7, −0.8 and −0.9 respectively) within the areas occupied by dab, but no significant correlations were detected within the larger spatial range of plaice.

Parameter	Estimate	Std. error	t value	*p*	DoF	Residual deviance	% Expl
Dab condition							
NULL					221	8.80	
Intercept	1.744	0.106	16.501	<0.001			
Malacostracans density (log)	0.054	0.023	2.385	0.0183	220	7.26	
Crab density (log)	−0.108	0.038	−2.828	0.0053	219	6.96	
Year 2009	0.088	0.029	3.022	0.0036	218	4.02	
Polychaete density (log)	0.164	0.044	3.729	<0.001	217	3.84	
Depth	−0.047	0.012	−3.883	<0.001	216	2.97	
Organic content	−0.193	0.047	−4.106	<0.001	215	2.39	
RESIDUAL						2.39	72.85
Plaice condition							
NULL					1252	40.76	
Intercept	1.813	0.021	84.330	<0.001			
Crab density (log)	−0.061	0.021	−2.916	0.0036	1251	40.76	
Malacostracan density (log)	−0.024	0.008	−2.899	0.0038	1250	40.22	
Year 2009	0.209	0.015	13.723	<0.001	1249	21.51	
RESIDUAL						21.51	47.23

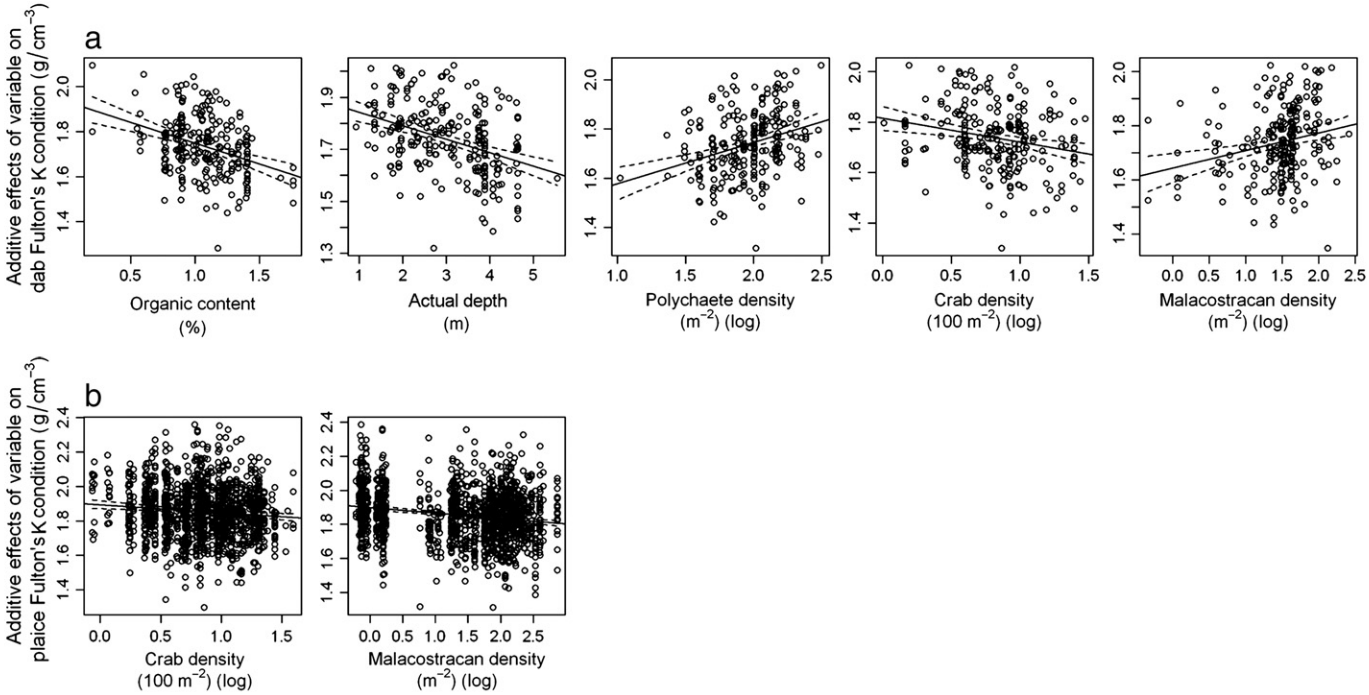

Fig. 6. (a) GLM plots showing additive effect of each significant variable on Fulton's K condition of all dab caught (n = 222) over four sites and between June and September in two years, (b) GLM plots showing additive effect of each significant variable on Fulton's K condition of all plaice caught (n = 1253) over four sites and two years during the post-settlement period.

Rosenberg, 1978). Anthropogenic inputs of organic matter in coastal bays could therefore have a negative impact on flatfish nursery areas.

Macroalgal cover in Galway Bay had a negative effect on plaice density; this corroborates laboratory evidence of plaice actively selecting substrata free of vegetation (Wennhage and Pihl, 1994) and field reports of reduced plaice densities in areas partly covered with algae (Pihl and Van der Veer, 1992). The effect is likely attributed to reductions in feeding efficiency (Nordström and Booth, 2007) since plaice are mostly dependent on sedentary infaunal prey (De Raedemaecker et al., 2011b). Macroalgae play an important functional role in structuring benthic faunal assemblages and alter their accessibility as food source. Despite the increase of some mobile epifauna under algal cover, there is a general tendency of decreased numbers of sedentary sediment-water interface feeders (especially bivalves and tube-dwellers) and prey availability (Everett, 1994). A relationship between algal cover and dab density was not detected and, to our knowledge, has not been previously recorded in the literature. Interspecific differences in the use of intertidal areas, foraging behavior and dominant prey type might explain the different effect of macroalgal cover on densities of the two flatfish species. Although the mechanisms (e.g. mortality due to anoxic condition, active avoidance, reduced prey availability) underlying low plaice densities in algal covered habitats in Galway Bay are uncertain, the effect could result in decreased recruitment (Pihl et al., 2005). As a consequence of increased eutrophication in shallow waters, nursery grounds are more often covered by fragmented and detached drifting vegetation (Pihl et al., 2005) which can decrease habitat complexity and cause severe oxygen deficiency if persistent in an area (Norkko and Bonsdorff, 1996). Management actions are therefore crucial to prevent deteriorating coastal habitats and the presence of algal mats in nursery areas.

4.3. Biological mechanisms affecting variability in density and condition

Predation, which is perhaps the most important cause of flatfish mortality during the post-settlement phase (Bailey, 1994), affected flatfish distribution and condition in Galway Bay. Dab densities were lower in areas with high shrimp densities, consistent with observations in the Thames estuary where shrimp predation has been postulated as a controlling factor in juvenile dab abundance (Power et al., 2000). The effect may be linked with predator avoidance as suggested by laboratory evidence that settling fish spend less time on sediments where predators are present (Wennhage and Gibson, 1998). Surprisingly, plaice densities in Galway Bay were positively correlated with shrimp densities. This may be because both demersal species were attracted to sites with abundant food supply or other favorable environmental conditions. The higher proportion of larger plaice compared to dab may explain their lower vulnerability to shrimp predation. Reduced plaice and dab condition at sites with higher crab densities was also revealed. This is in accordance with results of Burrows and Gibson (1995) which showed reduced activity levels and feeding success of plaice in the presence of predators. Maia et al. (2009) also observed sub-optimal foraging of *S. senegalensis* by the presence of a predator and this would inevitably reduce fish condition. Predator–prey interactions are determined by size ratios (Ellis and Gibson, 1995) and laboratory experiments carried out by van der Veer and Bergman (1987) found that plaice have a size refuge from predation by *C. crangon* at 30 mm, and from *C. maenas* at 50 mm. The majority of the fish sampled in Galway Bay were over 30 mm and this might explain why shrimp densities, in contrast to crab densities, did not feature as a significant variable in models explaining flatfish condition. A long-term study in the west of Scotland was also unable to detect evidence for control of plaice populations by shrimp predation (Burrows et al., 2001).

There was no evidence of inter- and intra-specific competition negatively influencing the density and condition of either species, implying that flatfish densities did not exceed the carrying capacity of the nursery grounds in Galway Bay. This is in contrast to other studies in the Irish Sea where density-related processes on juvenile plaice may occur (Nash and Geffen, 2000). However, these studies have reported densities between 0.4 m^{-2} and 3 m^{-2}, substantially higher than the densities observed in Galway Bay.

4.4. Nursery habitat quality in Galway Bay

Juvenile plaice and dab from two years and four distinct nursery areas in Galway Bay showed spatial variation in Fulton's condition and density but no uniform trends were revealed for both species. Certain nursery areas showed consistently higher growth or density over the years but it was unclear whether these differences arose as a result of differences in larval supply and topographic features of the shore line (Pihl et al., 2000) or due to processes acting on the juvenile life stage. Longer time series could elucidate the nature of the mechanisms underlying this pattern. Future research should determine the relative importance of each nursery area by their overall contribution (and contribution per unit area) of juvenile flatfish recruiting to the adult stock (Beck et al., 2001; Dahlgren et al., 2006). Either way, it is important to identify these nursery areas with a high survival rate of juvenile flatfish and consider them appropriately in coastal zone management.

4.5. Conclusion

This study provides a comprehensive look at how biotic and abiotic habitat characteristics influence the Fulton's K condition and density of two important flatfish species. The interaction of various substrate features showed the complex nature of these highly dynamic nursery areas. Habitat use of plaice and dab in Galway Bay was primarily influenced by depth but predation pressure and feeding opportunities clearly contributed to Fulton's K condition differences between nurseries. This study also illustrates how distinct sets of habitat features can drive spatial variation in density and condition of juvenile flatfish highlighting the value of studying both variables when modeling habitat requirements. Knowledge gained about the quality of nursery habitat for commercially important fish species provides a basis for mapping essential flatfish habitats to elucidate the causes of survival and recruitment variability and to inform management plans for coastal areas.

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