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Larval Fish Assemblages on Ireland's West Coast: Insights into Long-Term Community Shifts

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ABSTRACT

This study aimed to maximize the value of historical ichthyoplankton data from the Mackerel Eggs Survey (MEGS) by examining changes in fish larval communities over a nine-year interval (2007 and 2016) along the west coast of Ireland. Larval distribution and composition in on-shelf and off-shelf areas were assessed using a GULF VII plankton sampler towed at four knots along a V-shaped transect. Sampling was conducted approximately five metres above the seabed, or to a maximum depth of 200m. A total of 1,397 fish larvae were collected in 2016 and 499 in 2007. In 2016, 43 species from 25 families were identified, compared with 27 species from 19 families in 2007. *Cyclothone braueri* (garrick) was the most abundant species in 2016, while *Entelurus aequoreus* (snake pipefish) dominated in 2007. Multidimensional scaling (MDS) identified three distinct larval assemblages in 2016 and two in 2007. Multivariate statistical analyses confirmed significant interannual differences in community composition, driven largely by environmental conditions, with depth emerging as the most influential factor, closely associated with variations in temperature and salinity. Despite the temporal gap, the findings highlight the enduring value of archived plankton survey data for detecting long-term ecological changes in larval fish communities. Such insights are vital for understanding ecosystem variability, setting conservation priorities, and guiding sustainable fisheries management under changing oceanographic conditions.

INTRODUCTION

To understand the effects on different fish species, a deeper knowledge of spawning habitat characteristics is required **(Huebert & Peck, 2014; Ciannelli *et al.*, 2015; Macura *et al.*, 2016; Taylor *et al.*, 2019)**. Moreover, when considering climate change, the study of time-related assemblages should also be emphasized **(Asch, 2015; Lee *et al.*, 2021;**

Lima *et al*., 2022). Most studies exploring changes in marine fish distributions have focused on adult stages, while relatively little is known about changes in early life stage distributions—particularly the larval stage—especially on temporal scales **(Llopiz *et al*., 2014; Walsh *et al*., 2015; Munk & Lindegren, 2024)**. From 1951 to 2002, approximately half of the fish larvae taxa and distributions along the West Coast of the United States shifted, a change linked to climate change **(Wilson *et al*., 2016; Morley *et al*., 2018)**.

Changes in the timing of larval occurrence have also been associated with temperature changes in the English Channel, with a 13-year study showing larval occurrence shifts of 10–30 days depending on species **(Arula *et al*., 2019)**.

The Continuous Plankton Recorder (CPR) has been an important source of knowledge on larval fish in the Atlantic Basin **(Ostle *et al*., 2019; MBA, 2024)**, although detailed species abundance records have only recently become available. Historically, while the number of fish larvae in each sample was counted, they were not routinely identified to species or taxonomic group. Currently, a North Atlantic region atlas documents the seven most common fish larval taxa from 1948 to 2005, covering areas as far west as 20° **(Edwards *et al*., 2011)**. However, CPR gear is unsuitable for fast-swimming species or deep-water sampling, making other methods necessary for a complete understanding of plankton communities.

The west of Ireland lies in a "shadow" of CPR data coverage, meaning there is very little time-series information on plankton for this region. Fish larvae vary in size as they grow but are generally around 12mm in average length **(Edwards *et al*., 2011)**. Sampling methods target various size fractions of fish larvae and copepods, with flow meters measuring density per seawater volume. Oceanographic measurements, including CTD downcasts, are crucial for positioning sampling equipment accurately around frontal areas **(Xiao *et al*., 2023)**.

Several commercially important Northeast Atlantic species have shown a declining abundance trend in the CPR dataset from 1986 to 2005, including clupeids, mackerel, blue whiting, and cod **(Edwards *et al*., 2011)**. Assessing the temporal and spatial spawning distribution of fish larvae is essential, as they are highly vulnerable to environmental changes **(Ciannelli *et al*., 2015; Ijima & Jusup, 2023)**. Such assessments can estimate reproductive success, predict future catches of commercially important species, and monitor anthropogenic impacts of global warming on marine ecosystems.

This work should be considered in a multispecies context, as spawning habitat overlap and species-specific responses to environmental conditions are not always clear **(Laub & Budy, 2015; Taylor *et al*., 2019; van Leeuwen *et al*., 2023)**. At certain times, fish larvae may compete for food, with density-dependent effects influencing recruitment success **(Beukhof *et al*., 2019; Zimmermann *et al*., 2021)**.

The Mackerel Eggs Survey (MEGS) is part of a sampling series conducted every three years. Coordinated by the International Council for the Exploration of the Sea (ICES), it surveys Atlantic mackerel (*Scomber scombrus*) and horse mackerel (*Trachurus*

trachurus) between January and July along the eastern Atlantic from Gibraltar to Scotland's north coast. The goal is to estimate spawning stock biomass for these species in the northeastern Atlantic. The Marine Institute participates in this programme, with survey stations including the west of Ireland and the Celtic Sea **(ICES, 2014)**.

This study builds on the MEGS sampling opportunity, investigating differences in fish larval communities—particularly between on-shelf and off-shelf areas to the west of Ireland. It analyzes the spatial distribution and assemblage structure of fish larvae, exploring their relationships with oceanographic conditions (e.g., temperature, salinity, depth) and identifying potential spawning locations and reproductive strategies of adult fish from 2007 to 2016.

Although the dataset covers nine years, these historical records remain highly valuable, offering rare baseline information for assessing long-term ecological variability in temperate marine systems. The findings address a significant knowledge gap in the early life history of marine fish in Irish waters and highlight the need for sustained ichthyoplankton monitoring to detect community shifts under changing oceanographic regimes.

MATERIALS AND METHODS

Field sampling

A total of 64 samples were collected during two Mackerel Eggs Survey (MEGS) cruises conducted in the West of Ireland in 2007 and 2016. The sampling site coordinates were similar in both years (Fig. 1). Cruises took place from 3–21 June 2016 and from 5–15 July 2007. The ICES MEGS design employed an adaptive approach, with changes in effort over time that included a northward shift intended to define the extent of mackerel spawning, which appears to have increased in recent years **(Hughes *et al*., 2014)**.

The GULF VII plankton sampler was towed at four knots on a V-shaped profile at each station. Using a winch with an 11 mm co-axial cable in an armoured sheath, the GULF was deployed over the stern. The maximum sampling depth was 200 m or within five metres of the seabed. Each tow lasted 40 minutes. If a thermocline with a temperature difference greater than 2.5°C over a 10m depth was encountered, the tow was stopped 10m below the thermocline and the sampler recovered.

Onboard, the cod-end was removed after each tow, replaced with a second cod-end, and the plankton net washed down. The cod-ends were then transported to the vessel laboratory, where the plankton samples were rinsed out. A 4% buffered formalin solution was used to preserve the samples before they were returned to the laboratory for further analysis.

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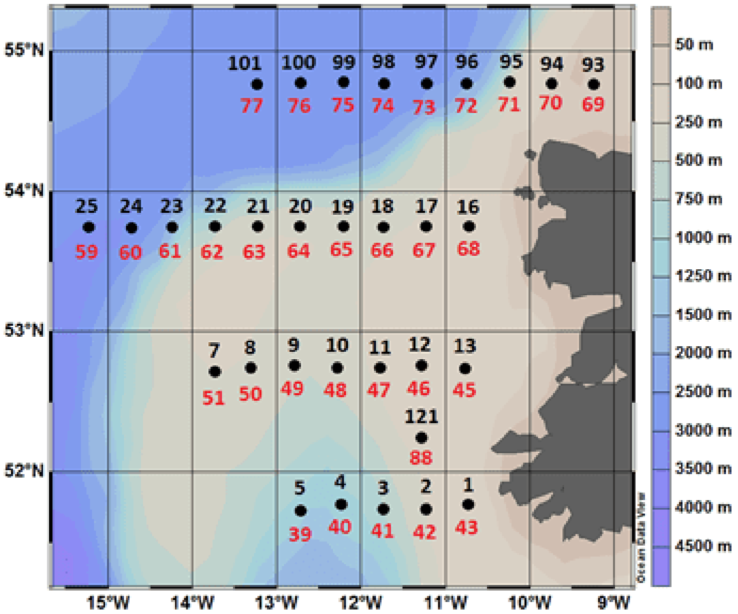


Fig. 1. Study area and stations sampled with the Gulf VII sampler during MEGS survey in 2007 and 2016. The black dot circles represent sampling stations which are numbered differently in each year. The numbers in black represent station numbers labelled in 2016 while red numbers represent station numbers in 2007. The vertical depth zonation on the right represents bathymetric depth.

Laboratory analysis

In the laboratory, all fish larvae (excluding those sorted onboard) were separated from other zooplankton and transferred into 85% ethanol. Using appropriate identification keys, the larvae were identified to the lowest possible taxon based on morphological characteristics, including the number of vertebrae and myomeres, pigmentation, body shape, supination, fin development patterns, fin placement, and eye shape **(Russel, 1976; Fahay, 1983; Re & Meneses, 2009; Bonecker *et al.*, 2019; Appleyard *et al.*, 2022; Reynalte-Tataje *et al.*, 2024)**. The number of fish larvae collected at each station was standardized as the count per 100m³ of seawater filtered through the GULF sampler.

Environmental data

A PRO-NET CTD and flow sensor was attached to the plankton net to record temperature, conductivity, salinity, and the volume of water filtered during each tow. The

PRO-NET electronics system is a sensor package for plankton samplers that enables data to be transmitted in real time via coaxial cable to a PC display onboard the sampling vessel or logged internally for later download. The standard sensor suite includes depth, temperature, salinity, internal flow (i.e., volume of water filtered), and external flow (used as an index of sampler efficiency).

In situ measurements of sampling depth (m), temperature (°C), and salinity collected at each station were processed using Ocean Data View v4.7.10 **(Schlitzer, 2017)** to produce vertical profiles. Prior to analysis, average values for temperature and salinity were calculated for each water column layer.

Standardization of data

Variation in depth, tow distance, and volume of water filtered occurred between hauls. Therefore, data were standardized before analysis. Following the method of **Smith and Richardson (1977)**, standardization was performed in terms of the volume of water filtered and the number of fish larvae collected in each sample.

$$\textbf{Volume filtered (m}^3\textbf{)} = \frac{\textbf{Flowmeter revs * Nose cone aperture * Efficiency factor}}{\textbf{Flowmeter calibration}}$$

Where,
Flowmeter revs = Revolutions number made by the flowmeter propeller during plankton net tow
Nose Cone Aperture = The area of the nose-cone aperture of the sampler in m^2 (πr^2)
Flowmeter-calibration = Flowmeter revolutions number per meter towed, gained from the flume or sea calibration in free flow

$$\textbf{Larvae m}^{-2} = \frac{\textbf{Larvae counted * Depth * Factor}}{\textbf{Volume filtered}}$$

Where,
Larvae counted = Number of larvae in the sample
Depth = the sampling depth, in metres
Factor = Raising factor from sub-sample to whole sample

Data analysis

For both years, statistical analyses were conducted to determine species contributions to station ordination, species abundance and composition in the fish larvae community, species spatial distribution, and potential relationships with oceanographic features in the study area. All analyses were performed using PRIMER v7.0.24.

A cohesive group of stations with similar taxonomic composition was identified using hierarchical clustering techniques. Ranked Bray–Curtis similarities were used to calculate the Similarity Profile (SIMPROF), a permutation test that clusters stations a priori into statistically significant groups. These ranks were compared with permutations of the expected family density data. For each branch of the cluster analysis, SIMPROF was calculated to determine whether the cluster was significantly different; if the π value exceeded the expected value, the grouping was considered significant ($P< 0.01$) **(Clarke & Gorley, 2015)**.

The similarity matrix of species community composition at various stations was visualized using non-metric multidimensional scaling (MDS) in a two-dimensional plot. Cluster analysis was used to identify groups of stations that aggregated at similar levels of similarity, and these groups were represented in the MDS plot using major similarity contours.

Analysis of Similarity (ANOSIM) was applied to test for differences in species composition among SIMPROF-generated station clusters both within and between years. ANOSIM produces a measure of site separation, R, where $R \approx 0$ indicates that similarities within and between sites are, on average, the same, and $R = 1$ indicates complete separation (all replicates within a site are more similar to one another than to any replicate from another site). ANOSIM also provides a *P*-value, with $P< 0.05$ indicating statistical significance **(Anderson & Walsh, 2013)**. When significant differences were detected with ANOSIM, Similarity Percentage Analysis (SIMPER) was used to identify the species contributing most to observed differences in assemblages between clusters and between years. SIMPER ranks species according to their percentage contribution to these differences, using a matrix derived from Bray–Curtis similarity coefficients calculated from transformed species abundance data **(Clarke *et al*., 2014)**.

BIO-ENV analysis was conducted to link biological distribution patterns to environmental variables **(Clarke *et al*., 2014; Giblin, 2017)**. This method calculates Spearman rank correlations between the biological similarity matrix (based on Bray–Curtis coefficients) and environmental similarity matrices (based on Euclidean distances) derived from all possible sequential combinations of measured environmental variables. The highest correlation value (best value) indicates the combination of variables that best explains the biological ordination **(Clarke *et al*., 2014)**.

RESULTS AND DISCUSSION

Environmental conditions

Overall, temperatures were higher in 2007 compared to 2016. The yearly difference was more pronounced at greater depths. For example, near-surface temperatures (3 m depth) in 2016 ranged from 13.1 to 15.5°C, while in 2007 they were slightly warmer, ranging from 13.9 to 15.9°C. At 20m in depth, temperatures in 2007 ranged from 13.6 to 15.3°C compared to 10.7 to 14.8°C in 2016. This trend was also observed at the maximum sampling depth.

The higher temperatures in 2007 may reflect the later sampling period that year (by one month) or could be related to interannual variability. Sea temperatures in the study area have been gradually increasing over recent decades; for example, **Casal and Lavender (2017)** reported a steady rise in sea surface temperature (SST) along Irish coastal zones. Since the 1980s, satellite and *in situ* observations have indicated a general warming trend of 0.3–0.4°C per decade in Irish waters, mirroring temperature increases over land **(Government of Ireland, 2021)**.

In 2016, temperature showed greater spatial and depth variability. At a depth of 20m, pockets of both cooler and warmer water were found adjacent to each other on the shelf north of Ireland. This pattern was not observed at 3m or at maximum depth. In fact, spatial patterns at 3m and maximum depth were almost the inverse of each other: the warmest temperatures tended to occur very close to shore at a depth of 3m, while at maximum depth they were found further south and west. In contrast, spatial patterns in 2007 were more consistent across depths, with warmer water pockets located further south or far west (off-shelf). At maximum depths, warmer waters covered a larger area in 2007 than in 2016, although temperature variation was less pronounced in deeper layers.

In addition, **Casal and Lavender (2017)** presented spatial distributions of average annual SST over a 34-year period (1982–2015), showing warmer waters in southern regions compared to northern Irish waters. They recorded the highest annual SST in 2007, matching the situation in the present study. Although their dataset did not extend to 2016, their results indicated a decrease in SST starting in 2007, which may also explain the lower temperatures observed in 2016. Seasonal effects also play a role, as **Casal and Lavender (2017)** found that SSTs in all ICES regions peak between July and September.

Nearshore estuaries and river plumes strongly influence the waters of continental shelves globally, contributing to high primary and secondary productivity and abundant fish larvae **(Smith & Simpkins, 2018; Blampied *et al.*, 2022)**. In the present study, lower salinity was recorded at stations nearshore at depths of 3 and 20m, reflecting the influence of the Shannon River, which—with a catchment area of 11,638km²—delivers a large freshwater input to Ireland's west coast **(Smith & Cave, 2012)**. Over longer timescales, coastal freshening may be associated with increased winter rainfall under global warming **(Nolan *et al.*, 2009)**. Salinity gradients were also detected at the shelf edge, near the northwest coast of Ireland, due to the Irish shelf front—a thermohaline front separating North Atlantic waters from Irish shelf waters **(Miller & Christodoulou, 2014)**. This front persists year-round, though its position varies seasonally and interannually.

Fish larvae density and composition

In 2016, fish larval density ranged from 20 to 219 individuals m^{-2}, with a mean of $82m^{-2}$ (Fig. 2). In 2007, densities ranged from 2 to $95m^{-2}$, with a mean of $24m^{-2}$ (Fig. 2a). In both years, larval density increased toward the northern part of the survey area. The highest abundances were recorded at the same station in both years, located on the continental shelf edge northwest of Ireland (Fig. 2, marked 'H'). Other high-density sites were also near the shelf edge. The lowest density in 2016 occurred off-shelf in the Rockall Trough to the northwest (Fig. 2b, marked 'L'), while in 2007 it was recorded in the south near the Porcupine Seabight (Fig. 2b, marked 'L').

In total, 499 fish larvae from 27 species (19 families) were sampled in 2007, and 1,397 larvae from 43 species (25 families) in 2016. Despite this diversity, certain species dominated. In 2007, *Entelurus aequoreus* (snake pipefish; family Syngnathidae) accounted for 59.3% of all larvae, followed by *Scomber scombrus* (Atlantic mackerel) at 11%. In 2016, *Cyclothone braueri* (Garrick; family Gonostomatidae) was most abundant (24.91%), followed by *S. scombrus* (22.26%).

Overall, the larval assemblage composition was similar to that reported in previous studies from the northeast Atlantic **(Ibaibarriaga *et al.*, 2007; Dransfeld *et al.*, 2009; Edwards *et al.*, 2011; Tiedemann *et al.*, 2014)**, though some species, unique to the North Sea and Celtic Sea, were recorded in those works. *C. braueri* was abundant in 2016 but scarce in 2007, with higher densities at the shelf edge or off-shelf, though it was also found on-shelf in some locations. This species is one of the most common in the northeast Atlantic **(Parzanini *et al.*, 2017; Bergamasco *et al.*, 2023)**, and is dominant in mesopelagic and bathypelagic zones of the Sargasso Sea, representing 47% and 41% of the total catch, respectively **(Harold, 2015)**. In fact, it accounts for 90% of all specimens captured from depths of 400–800m and is co-dominant with *Cyclothone pallida* between 400– 1,000m. While likely abundant locally in the eastern central Atlantic, *C. braueri* is not commercially exploited **(Harold, 2015)** and is therefore often underreported in sampling schemes focused on commercially important species.

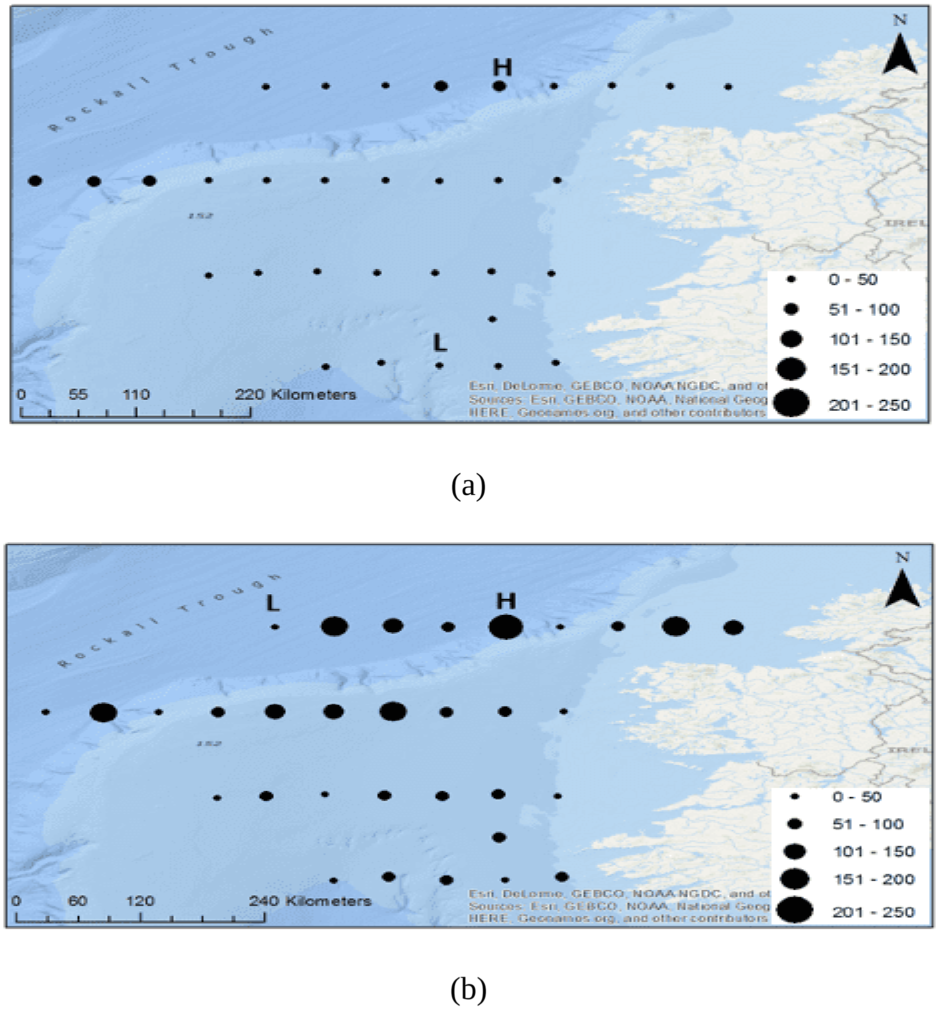


Fig. 2. Distribution of fish larval density (number of fish larvae per m^2) in the study area (a) 2007 and (b) 2016. H = highest density recorded, L = lowest density recorded.

In 2007, the fish larval assemblage was dominated by *Entelurus aequoreus* (snake pipefish) larvae. Higher densities were observed at continental shelf edge stations, lower densities occurred on the shelf, and almost no larvae were found near the coast. **Edwards *et al.* (2011)** reported that the abundance of this species increased from 2000 until 2005. Therefore, the high larval densities observed in 2007 in the present study were likely derived from large adult populations of *E. aequoreus* in the early 2000s **(Goncalves *et al.*, 2017)**. Trawl, plankton, and bird diet surveys indicated that the population size rose to exceptionally high levels until 2003 **(Harris *et al.*, 2007)**. After the mid-2000s, the population declined again **(Schultz, 2014)**, which is consistent with the low densities observed in 2016 in the present study.

The direct causes of this population boom remain unknown. During the outbreak, it was suggested that warmer surface sea temperatures might have increased reproductive success **(van Damme & Couperus, 2008; Goncalves *et al.*, 2017)**. However, this hypothesis does not account for the subsequent population decline.

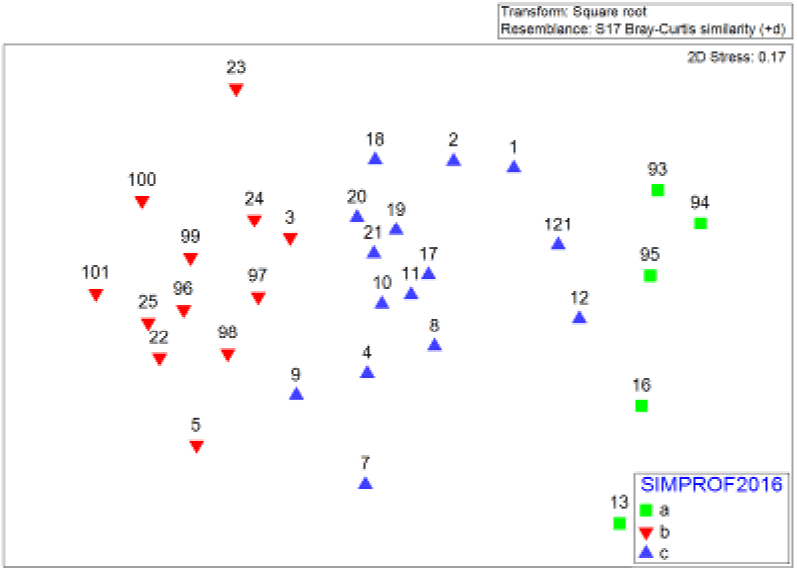
Spatial distribution of assemblages

In 2016, the MDS analysis indicated three distinct station groups based on Bray–Curtis similarity of fish larval assemblages (all depths combined), designated as ‘a’, ‘b’, and ‘c’ (Fig. 3a). Each group’s species composition was significantly different (Global ANOSIM R= 0.716, *P*= 0.001). The greatest dissimilarity was between group ‘a’ (coastal) and group ‘b’ (offshore and shelf edge), with pairwise analysis yielding R= 0.986, *P*= 0.001 (Fig. 3b). The lowest R value was between groups ‘b’ and ‘c’, where group ‘c’ was largely composed of on-shelf stations located seawards rather than near the coast (Pairwise R= 0.614, *P*= 0.001).

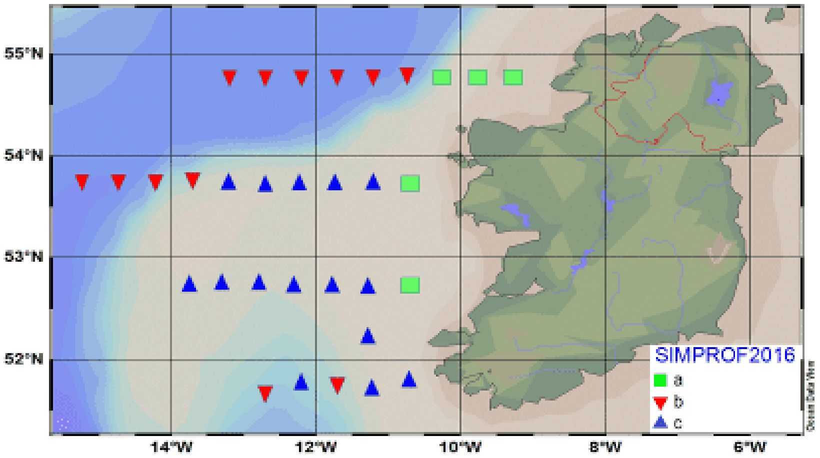
The 2007 MDS analysis indicated only two distinct larval assemblages (Fig. 4a), generally reflecting distance from the coast, with a few exceptions (Fig. 4b). One-way ANOSIM confirmed significant differences between these two station groups (R= 0.819, *P*= 0.001).

Assemblages were further examined using SIMPER analysis to identify species contributing most to the observed differences (Tables 1, 2). In 2016, seven species dominated group ‘a’ (coastal): *Lebetus guilleti* (Guillet’s goby), *Pomatoschistus microps* (common goby), *Scomber scombrus* (Atlantic mackerel), *Merluccius merluccius* (European hake), *Callionymus maculatus* (spotted dragonet), *Microstomus kitt* (lemon sole), and *Glyptocephalus cynoglossus* (witch flounder). Group ‘b’ (shelf edge and off-shelf) included *Cyclothone braueri* (in addition to *Benthosema glaciale*, glacier lanternfish), while *S. scombrus*, *C. braueri*, and *M. merluccius* also contributed to group ‘c’ (on-shelf seawards) along with *Gadiculus argenteus* (silvery pout).

Previous studies have found that fish larval assemblages are often distinguished along on-shelf/offshore gradients **(Giordano *et al.*, 2015; Koched *et al.*, 2015; Pattrick *et al.*, 2021)**, a pattern consistent with the present results. Assemblages can also be differentiated according to adult habitat **(Kent *et al.*, 2013; Zarrad *et al.*, 2013; Giordano *et al.*, 2015; Cuttitta *et al.*, 2018)**. Coastal group ‘a’ was characterized by demersal species such as *L. guilleti*, *P. microps*, *M. merluccius*, *C. maculatus*, *M. kitt*, and *G. cynoglossus*, all of which tend to prefer on-shelf waters. Although *S. scombrus* is a pelagic species, it contributed to the coastal assemblage in 2016 because spawning grounds in northwest Ireland are adjacent to a narrow shelf and therefore close to shore **(Dransfeld *et al.*, 2014)**.

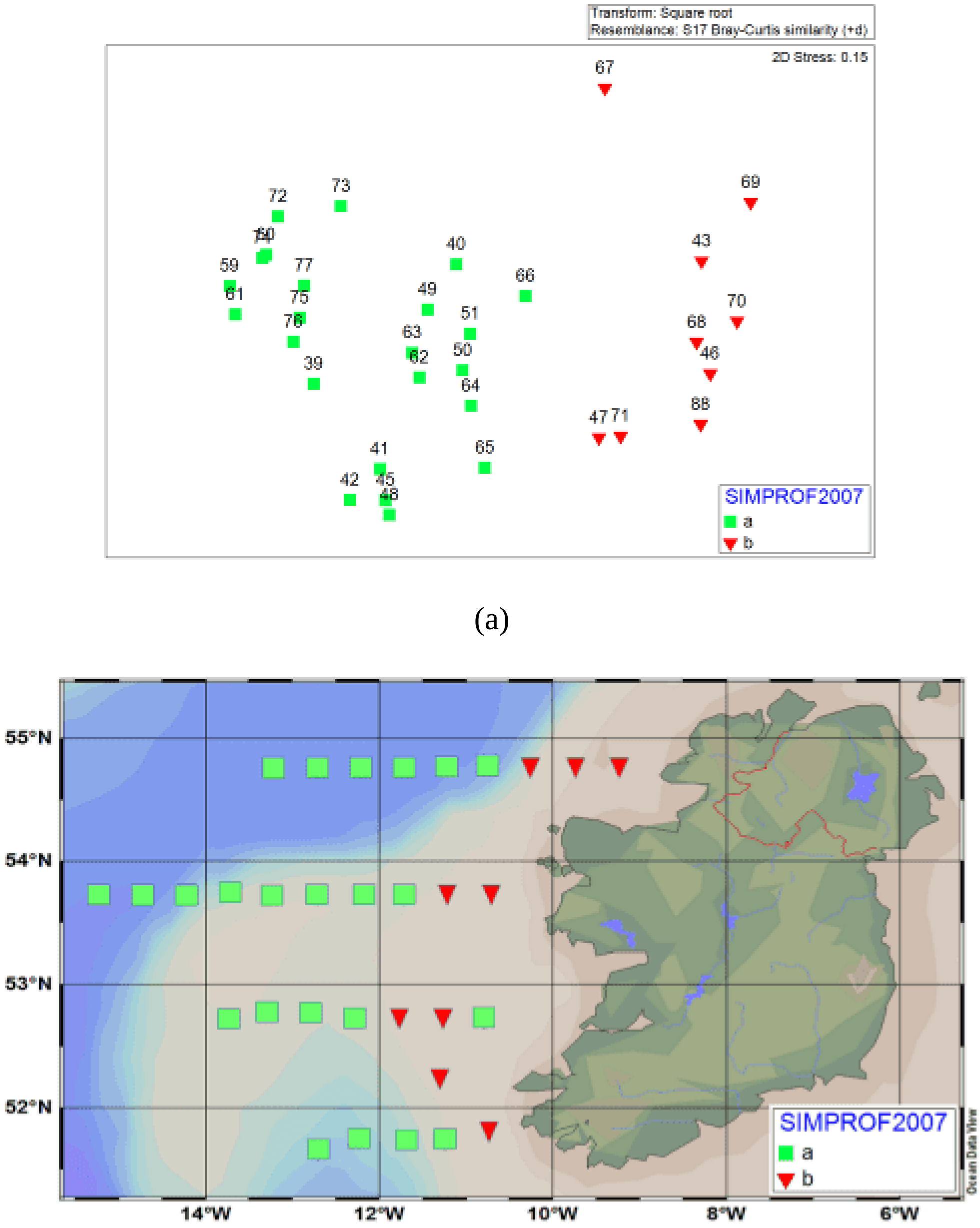


(a)



(b)

Fig. 3. (a) Multi-dimensional scaling (MDS) ordination representing fish larval community similarity from MEGS 2016 (all depths) at numbered stations and (b) geographical location of fish larval groups defined by MDS ordination. The stress value for MDS was 0.17.



(a)

(b)

Fig. 4. (a) Multi-dimensional scaling (MDS) ordination representing fish larval community similarity from MEGS 2007 stations (all depths) and (b) Geographical location of the larval fish assemblages for 2007 survey defined by MDS ordination. The stress value for MDS was 0.15.

The offshore and shelf-edge group ('b') in 2016 (Fig. 3) comprised two mesopelagic species: *Cyclothone braueri* and *Benthosema glaciale*. *B. glaciale* is an oceanodromous species typically found in high concentrations in deep waters, with densities decreasing in shallower areas **(Dransfeld *et al.*, 2009)**. Larvae of both species have previously been recorded in deep waters off the Irish coast at high abundance **(O'Brien & Fives, 1995; Acevedo *et al*., 2002)**.

The on-shelf but seawards-located group ('c') in 2016 (Fig. 3a) contained several species with varying habitat preferences: pelagic (*Scomber scombrus* and *Gadiculus argenteus*), mesopelagic (*C. braueri*), and demersal (*Merluccius merluccius*). Stations in group 'c' were located in an area with broad geographical and hydrographical variability, which may explain the mixture of species with diverse habitat preferences.

The high density of *S. scombrus* in this area was likely due to egg and larval drift onto the shelf from spawning aggregations concentrated along the shelf break **(Jansen, 2016; Arai *et al*., 2021)**, which contributed to the similarity values for group 'c' (Fig. 3a). *C. braueri* also featured in this group, although its distribution was lower compared to the off-shelf area. Two additional species, *G. argenteus* and *M. merluccius,* also contributed to group 'c' similarities, despite relatively low overall catches (n= 34 and n= 49, respectively), with percentage contributions of 8.47 and 7.93% (Table 2). These larvae were present at most continental shelf stations.

Table 1. SIMPER analysis showing the species that contribute to similarity within SIMPROF groups in 2007

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Group 'a'					
Entelurus aequoreus	2.97	29.88	2.06	75.01	75.01
Group 'b'					
Scomber scombrus	1.43	19.97	1.31	56.90	56.90
Callionymus maculatus	0.95	8.71	1.11	24.81	81.71

Table 2. SIMPER analysis showing the species that contribute to similarity within SIMPROF groups in 2016

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Group 'a'					
Lebetus guilleti	1.29	5.93	3.24	15.23	15.23
Pomatoschistus microps	1.57	4.94	0.75	12.70	27.93
Scomber scombrus	2.15	4.79	0.99	12.29	40.22
Merluccius merluccius	1.11	4.25	1.07	10.92	51.14
Callionymus maculatus	1.17	3.53	0.91	9.06	60.21
Microstomus kitt	1.26	3.35	1.11	8.60	68.81
Glyptocephalus cynoglossus	0.85	2.86	0.60	7.33	76.14
Group 'b'					

Cyclothone braueri	3.18	20.97	1.54	48.19	48.19
Benthosema glaciale	1.93	10.77	1.29	24.74	72.93
Group ‘c’					
Scomber scombrus	3.65	11.93	1.32	27.23	27.23
Cyclothone braueri	3.28	11.57	1.83	26.42	53.65
Gadiculus argenteus	1.25	3.71	1.18	8.47	62.12
Merluccius merluccius	1.30	3.47	0.96	7.93	70.05

In 2007, *Entelurus aequoreus* was the only species contributing to group ‘a’ stations due to its mass occurrence both on- and off-shelf. Its density declined closer to the coast, where stations formed group ‘b’, which contained only two species: *Scomber scombrus* and *Callionymus maculatus* (Table 1). The large-scale “invasion” of *E. aequoreus* in 2007 **(Harris *et al*., 2007; Kloppmann & Ulleweit, 2007; van Damme & Couperus, 2008; Goncalves *et al*., 2017)** likely influenced the degree of similarity separation between groups. *S. scombrus* recorded the second-highest catch after *E. aequoreus* in 2007, which is unsurprising given that the MEGS cruise design specifically targets *S. scombrus*. *C. maculatus*, which contributed to the group ‘b’ assemblage in 2007, is a demersal species that inhabits sandy bottoms, corresponding with the nearshore location of these stations.

The composition and abundance of fish larvae differed significantly between the two survey years (Global ANOSIM R= 0.553, *P*= 0.001). SIMPER analysis indicated that six species contributed most to the similarity in 2016: *Cyclothone braueri*, *S. scombrus*, *Benthosema glaciale*, *Electrona risso*, *Merluccius merluccius*, and *Myctophum punctatum*. In contrast, only two species—*E. aequoreus* and *S. scombrus*—contributed most to the similarity in 2007 (Table 3).

Referring to Table (3), the key species contributing to similarities between years were largely consistent with those listed in Table 2 (2016 SIMPROF groups) and Table 1 (2007 SIMPROF groups), except for the presence in 2016 of *E. risso* (electric lanternfish) and *M. punctatum* (spotted lanternfish). Both species belong to the family *Myctophidae* (lanternfishes), which inhabit both mesopelagic and oceanic zones and are common in the eastern Atlantic.

Table 3. SIMPER analysis showing the species that contribute to similarity within SIMPROF yearly groups

Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Group ‘2007’					
Entelurus aequoreus	2.13	15.24	0.84	56.29	56.29
Scomber scombrus	0.91	6.55	0.6	24.19	80.48

Group '2016'					
Cyclothone braueri	2.73	10.72	1	35.2	35.2
Scomber scombrus	2.3	5.52	0.78	18.14	53.34
Benthosema glaciale	0.87	1.87	0.37	6.13	59.47
Electrona risso	1.02	1.7	0.41	5.57	65.04
Merluccius merluccius	0.78	1.43	0.5	4.7	69.74
Mytophum punctatum	0.84	1.33	0.36	4.36	74.1

Linking fish larvae community with environmental variables

In 2016, the ordination was highly stable across all depths. At 3m deep, there was a strong relationship between community assemblage, bathymetry, and salinity, which explained why group 'b' stations were located off-shelf and at the shelf edge. A pronounced temperature gradient was also associated with bathymetry, with warmer waters on the shelf and cooler waters off-shelf. All environmental variables were statistically significant (BIO-ENV, Table 4). At a depth of 20m, bathymetry and salinity remained positively correlated with the shelf-edge and off-shelf group ('b'), but temperature was not statistically significant (BIO-ENV, Table 4). These results indicate that environmental associations with fish larval densities at the surface differed from those observed at greater depths, particularly in the role of temperature, which was less important deeper in the water column.

In 2007, ordination was also stable across all depths, although the specific environmental variables that were significant varied by depth. The relationship with bathymetry was less clear than in 2016; however, bathymetry and salinity were still significant at both 3 and 20m (BIO-ENV, Table 4). Approximately half of the stations located furthest from shore (with a few exceptions) showed a strong relationship with bathymetry and salinity (group 'a'), while stations nearer the coast (group 'b') were more closely associated with temperature—although in this case, temperature was not statistically significant (BIO-ENV, Table 6). Despite 2007 being generally warmer than 2016, temperature only showed notable explanatory power at the maximum sampling depth.

Table 4. BIO-ENV analysis showing environmental variable combination from 3 metres, 20 metres and maximum sampling depth in every sampling year

	Year			
	2007		**2016**	
Depth	**Combination variables**	**Correlation value**	**Combination variables**	**Correlation value**
3m	*Sal, Depth	0.579	*Temp, Sal, Depth	0.663
	Sal	0.548	Temp, Sal, depth	0.643
	Sal, Depth	0.521	Sal, Depth	0.598
	Temp, Sal, Depth	0.471	Sal	0.530
20m	*Sal, Depth	0.569	*Sal, Depth	0.611
	Sal	0.544	Temp, Sal, Depth	0.561
	Sal, Depth	0.519	Sal, Depth	0.548
	Temp, Sal, Depth	0.483	Sal	0.486
Max depth	*Temp, Depth	0.401	*Sal, Depth	0.492
	Sal, Depth	0.399	Depth	0.492
	Temp, Sal, Depth	0.376	Temp, Sal, depth	0.439
	Depth	0.347	Depth	0.364

The best variable combinations are marked with an asterisk (*) ($P< 0.001$). Temp: Temperature, Sal: Salinity, Depth: Depth

Based on this analysis, temperature, salinity, and depth are suggested to influence species composition **(Marium *et al.*, 2023)**. However, these relationships vary with depth, consistent with findings from prior studies **(Dransfeld *et al.*, 2009; Tiedemann *et al.*, 2014; Cuttitta *et al.*, 2016)** postulating that water depth is a key factor shaping species composition. The effects of water mass structure and movement on assemblage patterns and geographic distribution have been demonstrated by **McKinnon *et al.* (2015)** and **Rodriguez (2019)**. While **Çoker and Cihangir (2015)** discussed how differences in species life history and spawning patterns can influence larval fish assemblages. Assemblages are also affected by variability in water mass and movements near the shore, which relate to local bathymetry, distance from shore, wind forcing, and other physical factors **(Pattrick & Strydom, 2014; Siddon *et al.*, 2018)**. Additional influences include oceanographic features such as fronts, eddies, seasonal variation, and timing of sampling **(Paulic & Papst, 2013; Díaz-Astudillo *et al.*, 2019)**, all of which can alter assemblage distributions and therefore assemblage boundaries.

Adult spawning strategy (demersal vs. pelagic) can also influence larval fish distribution and assemblage structure **(Çoker & Cihangir, 2015; Alvarez *et al.*, 2021; Gavriilidis, 2022)**, sometimes leading to a phenomenon known as adaptive convergence—where larvae of different species occur together due to similarities in their life histories **(Siddon *et al.*, 2018; Goldstein *et al.*, 2019; Leal-Cardin *et al.*, 2024)**. Several factors can lead to the grouping of co-occurring fish larvae species:

1. Similarities in adult reproductive patterns **(Abrantes *et al*., 2015)**,
2. Exposure to similar hydrographic processes, such as currents or upwelling **(Rodriguez *et al*., 2015)**, or
3. Convergence toward a shared resource, such as a common feeding environment (e.g., zooplankton) **(Apango-Figueroa *et al*., 2015)**.

These associations are not fixed in time or space; rather, they are flexible and inherently sensitive to environmental disturbances **(Siddon *et al*., 2018; del Pilar Echeverri-García *et al*., 2022)**. The composition of larval assemblages, particularly their dominant species, often reflects the spawning strategies of the adults. For example, *Cyclothone braueri* is a pelagic, short-lived, semelparous species, with females maturing and spawning for the first time in their second year. Spawning occurs seasonally at high latitudes but tends to be more protracted at lower latitudes **(Harold, 2015)**. According to **Rabbaniha *et al*. (2015)**, larvae of most pelagic spawners are buoyant at hatch, resulting in a relatively uniform distribution even when spawning grounds are geographically distinct. This trait makes pinpointing the spawning locations of *C. braueri* challenging but explains its widespread distribution in the study area. *C. braueri* is known to occur abundantly across the northeastern Atlantic Ocean **(Sutton *et al*., 2013; Parzanini *et al*., 2017)**. The present study found similar results, with *C. braueri* being the most frequently captured and most abundant species in 2016, although its densities were lower in coastal assemblages. Higher larval densities for this species were recorded at higher latitudes in 2016.

In contrast, in 2007 *Entelurus aequoreus* was the most abundant species collected. Sampling that year took place one month later, so the difference in dominance between *C. braueri* (2016) and *E. aequoreus* (2007) could simply reflect differences in spawning timing. Temporal variation in species composition is common in marine ecosystems, often driven by reproductive cycles **(Wang *et al*., 2019; Olivar *et al*., 2022)**.

E. aequoreus has unique spawning behavior: females transfer eggs to males, which then care for them until hatching **(Schultz, 2014)**. Historically, the species was considered pelagic and oceanic, but by the mid-20th century, catches were more often reported from coastal waters **(van Damme & Couperus, 2008)**. However, large catches from pelagic waters were also recorded during plankton surveys in 2004 **(Kloppmann & Ulleweit, 2007; Goncalves *et al*., 2017)**, suggesting that environmental changes may have driven its mass occurrence in deeper oceanic waters—possibly resembling early 20th-century patterns **(Goncalves *et al*., 2017)**. **Pihl *et al*. (2006)** and **Moksnes *et al*. (2018)** proposed that *E. aequoreus* is commonly associated with seagrass beds and is negatively impacted by their loss and fragmentation in parts of the northeast Atlantic, including Sweden, due to nutrient loading, siltation, and physical disturbance.

Feeding success and predation are also critical considerations **(Pepin *et al.*, 2014)**. For example, **Koul *et al.* (2021)** linked declines in North Atlantic cod populations to reduced feeding success caused by lower copepod abundance under climate change. Predation on fish eggs and larvae is believed to be a major cause of mortality, exerted by numerous organisms **(Dembek *et al.*, 2019)**. Factors influencing predation include starvation levels **(Huebert & Peck, 2014)**, larval size and age **(Kerr *et al.*, 2015)**, predator density **(Goatley *et al.*, 2017)**, ontogenetic stage **(Takasuka *et al.*, 2017)**, temperature, and developmental rate **(Asch *et al.*, 2019)**.

CONCLUSION

In conclusion, the composition of fish larval assemblages in the study area differed markedly between 2007 and 2016, with *Entelurus aequoreus* (pipefish) dominant in 2007, while *Cyclothone braueri* was the most frequently captured species in 2016. The precise causes of the boom-and-bust cycles in *E. aequoreus* remain unknown, though they appear to be linked to environmental factors. Bathymetry was an important determinant of community similarity in fish larval assemblages, while the influence of temperature and salinity varied with sampling depth.

Scomber scombrus was considerably more abundant in 2016, despite sampling occurring a month earlier than in 2007. Coupled with a more advanced size and developmental distribution, this suggests an altered phenology of *S. scombrus* across the study area within a relatively short period (nine years). There is also some evidence of a northward shift in its distribution, although this remains contentious, as seasonal and other factors may obscure detection.

Larval fish assemblages in the study area are structured along an inshore–offshore gradient and shaped by the interaction between the spawning behaviour of resident marine fishes and local oceanographic features. For sustainable management, it is essential to recognise the distinctiveness of these habitats and communities, and to manage human activities at this spatial scale.

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DECLARATION

Competing interests

The authors declare no competing interests.

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