

# Impacts of the match-mismatch hypothesis across three trophic levels—a case study in the North Sea

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Sustainable fishery practices require accurate predictions of fish recruitment—the abundance of a new year class entering a fishery. A key driver of recruitment is the impact predator-prey dynamics experienced during early life stages has on their survival at later stages, as in the Match-Mismatch Hypothesis (MMH). MMH states that predator survival depends on the match (or mismatch) between the timing of predator feeding and that of prey availability. This study aims to understand how predator-prey spatio-temporal overlap explains the variation in a pelagic fish population. We explore the predator-prey overlap between each pair of three trophic levels in the North Sea (NS) from 1982–2017: herring (*Clupea harengus*) larvae, zooplankton (*Temora longicornis*, *Oithona* sp., *Pseudocalanus* spp., and *Acartia* spp.), and a phytoplankton index. We found that MMH explained 23% of recruitment (1-year-old) of NS autumn-spawning (NSAS) herring, performed similarly (21–26%) when using different trophic levels, and that there was a spatial pattern in both the overlap and the negative relationship between the overlap and recruitment, similar to the variation of habitat use of NS herring. Our results characterize how the MMH, including spatial variability, plays in controlling herring recruitment, while also considering unexplained variation for future study.

**Keywords:** fish recruitment, phenology, plankton dynamics, seasonal cycles.

## Introduction

Sustainable fisheries are necessary to sustain the growing human demand for protein (FAO, 2018). In order to reach sustainable harvest practices, fisheries scientists have attempted for over a century to effectively and accurately predict the abundance of upcoming year classes entering a fishery, that is, recruitment (Hjort, 1914; Walters & Collie, 1988; Myers, 1998). This body of work has been highly focused on identifying the critical stage for recruitment determination (Cushing, 1975), including the vulnerable larval stage from internal (yolk-sac) to external feeding (first 20–30 d of life for North Sea (NS) herring larvae, Denis *et al.*, 2016), as newly-hatched larvae experience a change in growth, predation, starvation, and survival trade-offs (Myers, 1998; Yúfera and Darias, 2007). However, research on recruitment processes is challenging due to the high number and variability of potential drivers of recruitment with relatively low explanatory power (Hjort, 1914; Walters and Collie, 1988; Myers, 1998; Rice and Browman, 2015). Solving the recruitment estimation problem is directly relevant to EAFM and to developing adaptation strategies to climate change, and it “is as relevant today as it was >100 years ago” (Rice and Browman, 2015), especially when, nowadays, the main focus is on overexploitation.

A potential key driver of recruitment is described in the Match-Mismatch Hypothesis (MMH), which states that a critical factor determining predator survival is the match (or mismatch) between the timing of predator feeding and that of prey availability (Hjort, 1914; Cushing, 1990; Durant *et al.*, 2013). When phytoplankton and zooplankton production overlap (match), fish larvae (ichthyoplankton) are more likely to survive due to high food availability and reduced predation

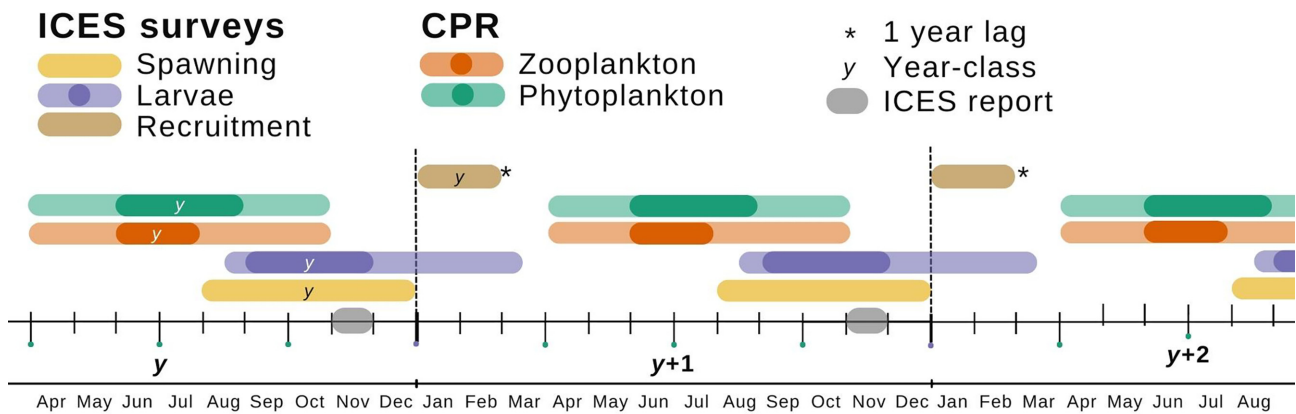
pressure through faster growth and higher food availability for the predator (Cushing, 1990; Durant *et al.*, 2007; Durant *et al.*, 2013).

MMH studies provide insight into the ecosystem state (species’ abundance and composition) and dynamics (energy transfer between trophic levels) (Brosset *et al.*, 2020; Ferreira *et al.*, 2020; Laurel *et al.*, 2021; Endo *et al.*, 2022). However, such studies generally only provide correlative support at specific locations, species, and/or trophic levels. Relevant advances in MMH studies have been made more recently, in particular on Northwest Atlantic mackerel (Brosset *et al.*, 2020), Pacific cod (Laurel *et al.*, 2021), and Northeast Arctic cod (Ferreira *et al.*, 2020; Endo *et al.*, 2022). Still, having a useful predator-prey metric that accounts for time and space while also working as a strong link between phenology and recruitment at multiple trophic levels is missing.

Assessing the relationship between the predator-prey overlap metric and recruitment requires a vast pool of data that can successfully capture the seasonal cycle of the biological community in a particular region. In the present study, we focus our efforts towards the NS, which is a region with an extensive pool of high-resolution data, including phenological characteristics of NS herring (*Clupea harengus*) larvae, small copepods, and phytoplankton. As expressed by Denis *et al.* (2016), NS herring is a key species in the NS ecosystem and is part of the basis of several ecological theories regarding the role of the larval stage in recruitment regulation (Cushing, 1969; Iles and Sinclair, 1982; Houde, 2008). Even though NS herring stock dynamics of herring are well studied, key questions remain about its recruitment dynamics (Payne, 2010), making it an ideal study species for this work.

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**Figure 1.** Timeline of data collection and how it affects calculations for the NSAS herring stock, as reported in ICES (2021).  $y$  denotes year-class, that is, the year the fish were born. \* denotes a 1-year-lag applied to the reported recruitment index at 0 wr (wr), which corresponds to 1-year-old fish for NSAS herring. Darker colours denote the timeframe of the peaks, whereas lighter colours denote the timeframe of the blooms of each of the organisms for the four spawning components of the NSAS herring stock (Orkney-Shetland, Buchan, Banks, and Downs, Payne, 2010; ICES, 2021).

NS herring spawns in both spring and autumn along the western NS. The NS autumn-spawning (NSAS) herring is composed of four spawning components with distinct spawning locations (Orkney-Shetland, Buchan, Banks, and Downs) and times (August to December) (Orkney-Shetland, Buchan, Banks, and Downs, from North to South) (Payne, 2010). This highlights that the relationship between space and time is worth considering, since the conditions these larvae face may have great implications to their survival into later stages. The eggs are benthic, whereas the newly-hatched larvae (about 6–9 mm) rise to become planktonic (Dickey-Collas *et al.*, 2010). Small herring larvae prey upon small copepod species, such as *Temora longicornis*, *Oithona* sp., *Pseudocalanus* spp., and *Acartia* spp. (Lusseau *et al.*, 2014; Alvarez-Fernandez *et al.*, 2015; Denis *et al.*, 2016; Wilson *et al.*, 2018), which, in turn, feed on phytoplankton. Having estimates of both phytoplankton and zooplankton variability provides a better chance of capturing relevant variations in the prey field. These three trophic levels (ichthyoplankton, zooplankton, and phytoplankton) represent a simplistic trophic chain and allow for the assessment of how these organisms interact with each other and the surrounding environment, as well their phenology dynamics.

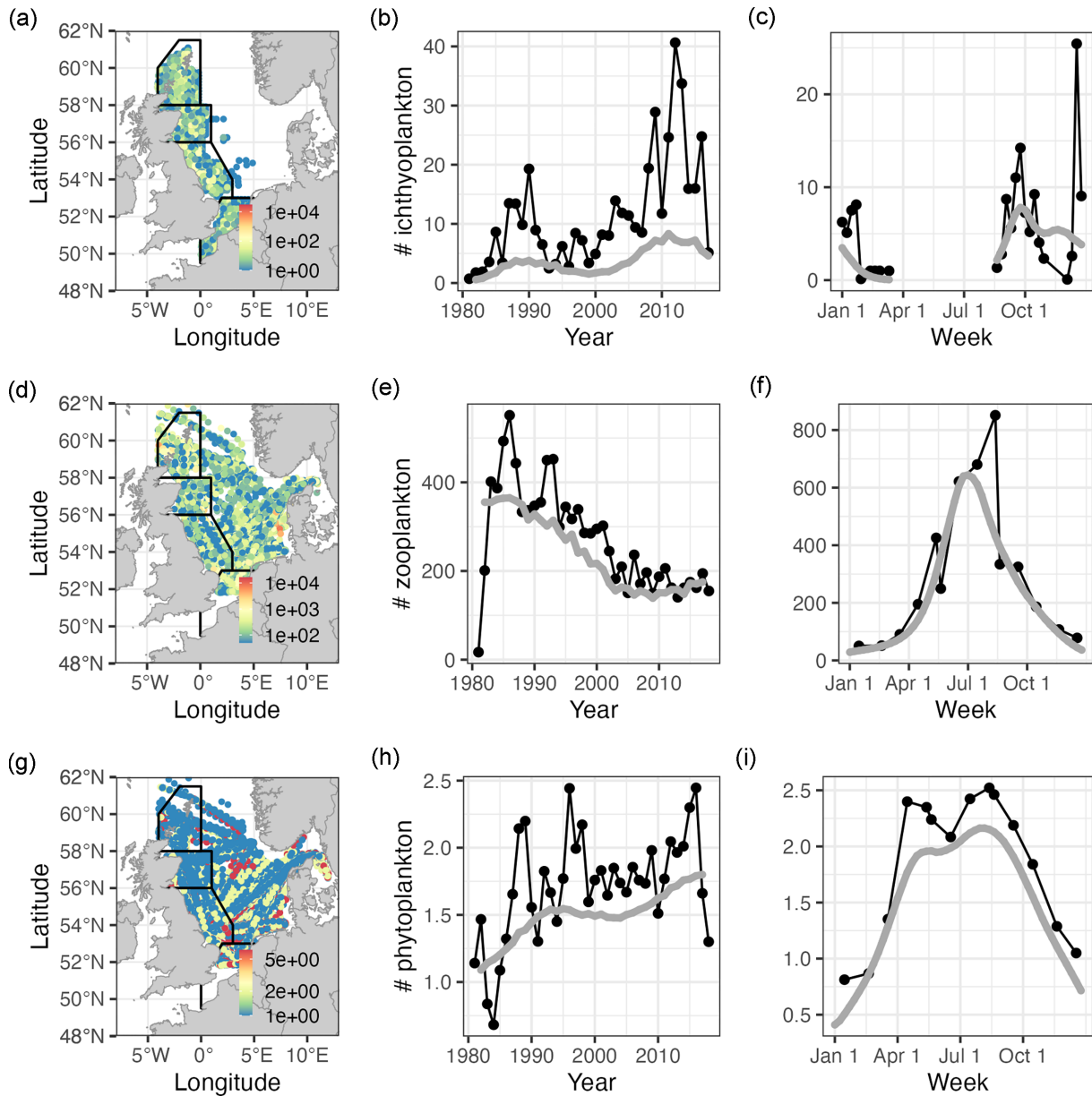
In this study, we aim at assessing the mechanistic applicability of MMH on three critical components: the importance of how MMH impacts recruitment variability in space; a multiple trophic level approach that represents true ecosystem complexity; and the extent to which MMH is relevant for predictions of future recruitment. These components represent key knowledge gaps and challenges in MMH research that we aim at filling by applying the methodology developed by Ferreira *et al.* (2020). To do so, we test the following hypotheses: (H1) predator-prey overlap explains recruitment of NS herring, (H2) there is a spatial pattern in the overlap, and (H3) there is a spatial pattern in the relationship between the overlap and recruitment. We focus on three trophic levels in the NS: herring (*C. harengus*) larvae, zooplankton (*T. longicornis*, *Oithona* sp., *Pseudocalanus* spp., and *Acartia* spp.), and a phytoplankton index, and explore the predictability of the predator-prey overlap metric against the recruitment of NS herring.

## Methods

### Data

The NS herring (*C. harengus*) larvae data were gathered from 1982 to 2017 from the ICES eggs and larvae database freely available online (Figure 1). These data were collected within the International Herring Larvae Survey (IHLS) (Gröger *et al.*, 2001). The data were collected using Gulf III and Gulf VII samplers with a 280 or 300  $\mu\text{m}$  mesh size net, sampled in an  $\sim 10$  by 10 nautical miles grid (ICES, 2010). We focused on the western NS, which is also where the NSAS stock spawns (Figure 1A, Payne, 2010). The highest recorded number of larvae occurred in 2011 and the lowest in 1981 (Figure 2B). The larval surveys for NS herring occurred from August to March (Figure 2C), thus representing both the spring- and the autumn-spawners, from which we only focus on the latter. We restricted the data to fish with length equal or above 6 mm (0.92% were thus removed) to include only feeding larvae. Denis *et al.* (2016) found a vacuity ratio (ratio of larvae with exhausted yolk) of 76% at 8 mm herring larvae from the Downs region. In our analyses, we considered larvae larger than 6 mm to guarantee that smaller feeding larvae (larvae with length between 6 and 8 mm, as found in Orkney-Shetland, Buchan, and Banks) were also included (Supplementary Figure S1). An upper threshold was not necessary since the larval length were  $\leq 36.5$  mm and only 0.0004% were  $\geq 30$  mm—the threshold at which they shift prey size and species (Supplementary Figure S1, Alvarez-Fernandez *et al.*, 2015; Denis *et al.*, 2016; Wilson *et al.*, 2018). As a measure of survival, we used recruitment of NSAS herring at 0 winter rings (wr), which corresponds to 1-year-old autumn spawning herring (ICES, 2021).

Both zooplankton and phytoplankton (Phytoplankton Colour Index, PCI) data were gathered from the Continuous Plankton Recorder database from the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) (Figure 1, Johns, 2020b, a). Zooplankton is represented by the abundance of *T. longicornis*, *Oithona* sp., *Pseudocalanus* spp., and *Acartia* spp. Even though *Calanus finmarchicus* has also been reported as one of the prey species of herring larvae (Last, 1989), we have not included this species as it has not been reported as a main prey species for the size classes we focus on by the most recent literature (Lusseau *et al.*, 2014; Alvarez-Fernandez *et al.*



**Figure 2.** Spatial (a, d, and g, logarithmic scale), interannual (b, e, and h), and seasonal distributions (c, f, and i) of the ichthyoplankton (a, b, and c), zooplankton (d, e, and f), and phytoplankton abundances (g, h, and i). The dark grey lines represent the predicted data (b, c, e, f, h, and i). Black polygons represent the following regions, from north to south, as in Payne (2010): Orkney-Shetland, Buchan, Banks, and Downs.

al., 2015; Denis et al., 2016). Furthermore, Nash and Dickey-Collas (2005) reported no clear relationship between the survival of young stages of herring and the abundance of *C. finmarchicus*. Additionally, as *C. finmarchicus* is a large copepod species that only becomes part of herring’s preferred prey from the size of 30 mm (Wilson et al., 2018).

Both zooplankton and phytoplankton are represented from 1958 to 2017 in the whole NS area (Figures 2d and g, respectively). Both types of organisms did not show a clear pattern in their interannual variability (Figures 2e and h, respectively). The zooplankton peaks in July or August (Figure 2f), whereas the phytoplankton shows a peak from May to August (Figure 2i).

Sea surface temperature (SST) data were downloaded from the National Oceanic and Atmospheric Administration (Reynolds et al., 2002). We used the optimum interpolation (OI) SST analysis, which is adjusted according to Reynolds et

al. (2002), and produced weekly on a one-degree grid taking into account sea-ice cover.

**Spatio-temporal modelling**

To conduct our analyses, we needed data series continuous in time and space (Ferreira et al., 2020). The sampling in the NS has been irregular in spatial and temporal coverage. Therefore, we needed to estimate the missing values and smooth the seasonal cycles. To do this, we used Generalized Additive Models (GAMs) to smooth and fill in the sampling-related spatio-temporal gaps as in Ferreira et al. (2020): using a GAM model fitted to the data, we projected the missing values creating a continuous spatio-temporal data set.

$$\log_e(A_{xy}) = \alpha + f_0(Week_y, Year_y) + f_1(SST_{xy}) + f_2(Lon_x, Lat_x) + \epsilon_{xy} \epsilon_{xy} \sim N(0, \sigma_{xy}^2) \quad (1)$$

**Table 1.** Performance of the three models used to characterize the seasonal cycle of each organism per year and location.

Organism	Model formulation	Dev. exp. [%] ( $r^2$ )
Ichthyoplankton	gam(fish~s(new_week,k = 5)+s(new_year,k = 5)+s(sst,k = 5)+te(LON,LAT,k = 5), family = poisson)	26.7 (0.06)
Zooplankton	gam(zoo~s(week,k = 5,bs = "cr")+s(new_year,k = 5)+s(sst,k = 5)+te(LON,LAT,k = 5), family = poisson)	29.1 (0.17)
Phytoplankton	gam(phyto~s(week,k = 5,bs = "cr")+s(new_year,k = 5)+s(sst,k = 5)+te(LON,LAT,k = 5), family = poisson)	18.6 (0.15)

Here,  $A_{xy}$ , represents either  $I_{xy}$ ,  $Z_{xy}$ , or  $P_{xy}$ , which is the abundance of ichthyoplankton, zooplankton, and phytoplankton, respectively, at location  $x$  and year  $y$ . The coefficient  $\alpha$  is the intercept. The 2-dimensional smooth function  $f_0$  of week (Week) and year (Year) estimates the average seasonal change in abundance. The smooth function  $f_1$  of SST provides the average change with SST. The 2-dimensional smooth function  $f_2$  of longitude (LON) and latitude (LAT) estimates the time-averaged spatial pattern. Finally,  $\varepsilon_{xy}$  is a normally distributed error term. All analyses were performed with the R statistical software (R Core Team, 2021).

The procedure for filling in the sampling-related spatio-temporal gaps for each of the three studied organisms reflects the number of zeros in each dataset, which was substantial: 72.22, 41.73, and 17.02% of the data were zeros, respectively, for ichthyoplankton, zooplankton, and phytoplankton (Table 1). Since the data are zero-inflated, we used a similar approach to Stige et al. (2015) in their Equations (4) and (5). Thus, the data were analysed using two statistical models (the hurdle model) to estimate  $I$ ,  $Z$ , or  $P$ : the dependant variable being either the presence/absence model quantifying the probability of sampling at least one organism at location  $x$  in year  $y$ ; or the abundance (log-transformation of  $I$ ,  $Z$ , or  $P$ ) for the locations with nonzero counts (Figures 2b, c, e, f, h, and i).

### Overlap modelling

We then calculated the *Overlap* metric from the curves (seasonal cycles averaged for each region) for the three trophic levels considered ( $I$ ,  $Z$ , and  $P$ ) as in Ferreira et al. (2020). The minimum integral of the areas of overlap under the curves of any predator-prey pair of trophic levels (phytoplankton/zooplankton,  $P/Z$ ; phytoplankton/ichthyoplankton,  $P/I$ ; or zooplankton/ichthyoplankton,  $Z/I$ ) served as the index of *Overlap*. The resulting *Overlap* index was standardized (from 0 to 1) to aid presentation following Equation (2).

$$\overline{Overlap}_{xy} = \frac{Overlap_{xy} - \min(Overlap_{xy})}{\max(Overlap_{xy}) - \min(Overlap_{xy})}, \quad (2)$$

where  $Overlap_{xy}$  is the predator-prey *Overlap*,  $\overline{Overlap}_{xy}$  is the normalized *Overlap*, and min and max represent the minimum and maximum values, respectively, of  $Overlap_{xy}$  for each pair of trophic levels for each location  $x$  and year  $y$ . Note that an index of 1 is not representative of a full *Overlap*, that is, the curves of both pairs do not necessarily fully overlap. The relationship between each pair and *Recruitment* (indicator of fish survival) of the herring ( $H$ ) was then assessed using a linear model (R Core Team, 2021) represented by Equation (3).

$$Recruitment_H = a + b \cdot \overline{Overlap}_{xy} + \varepsilon_{xy} \\ \varepsilon_{xy} \sim N(0, \sigma^2) \quad (3)$$

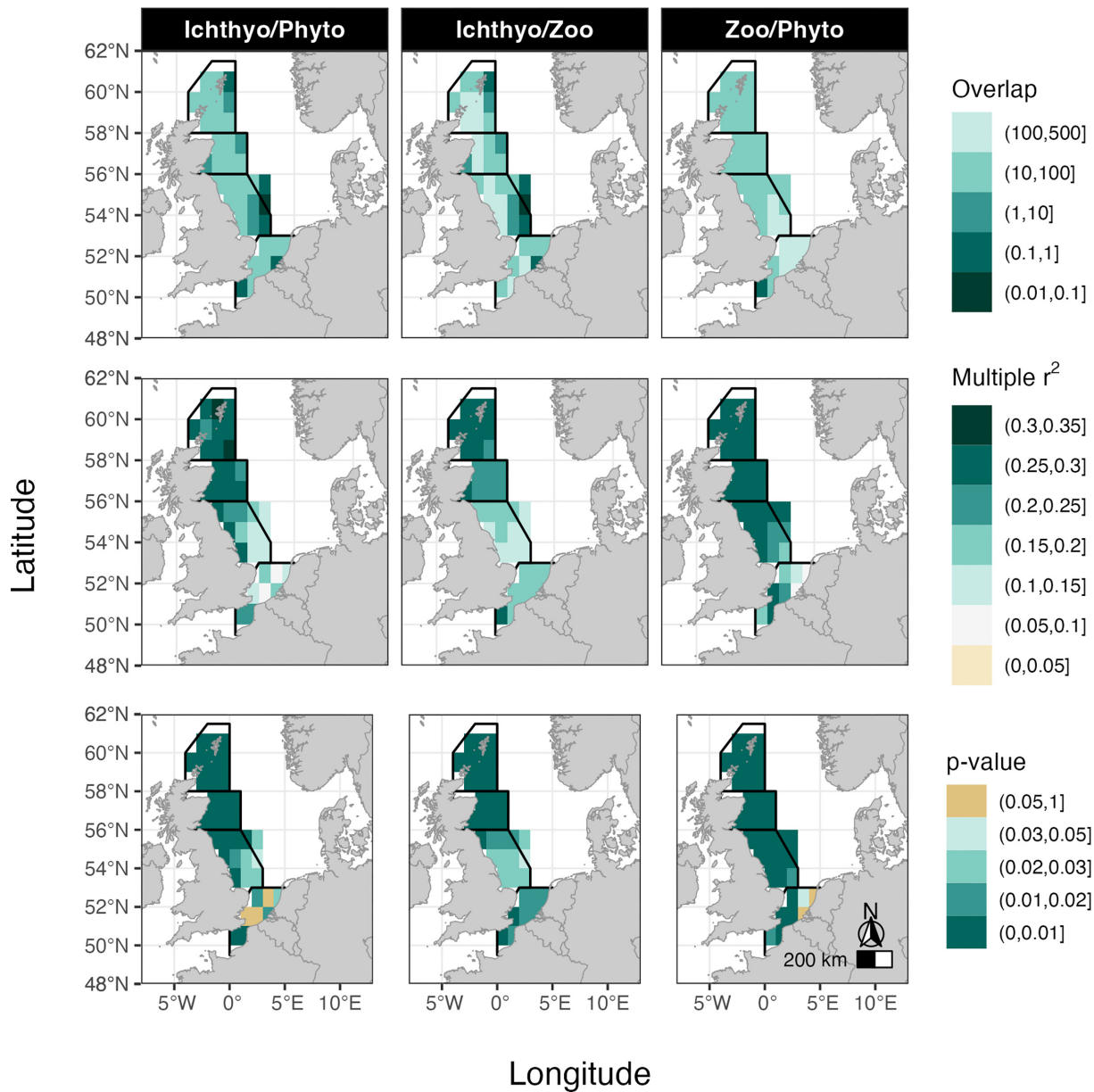
where  $Recruitment_H$  is the recruitment of NSAS herring at 0 wr (1-year-old fish) for the corresponding year-class (see Figure 1, ICES, 2021). We also estimated the predator-prey relationship for each pair regarding other phenology metrics. More details can be found in the Supplementary Material (Supplementary Figures S1 and S2).

### Results

The first objective of this study was to understand how the predator-prey spatio-temporal overlap at different levels of the food chain explains the variation in pelagic fish populations. The overlap metric provided information on the degree of spatio-temporal overlap between each pair (Figure 3, top section). This considers other aspects of the trophic chain, such as other phenology metrics (Supplementary Figures S2 and S3). The  $I/P$  pair presents a homogenous pattern of the *Overlap* index with a mean of  $16.9 \pm 10.7$  (Figure 3 top left). The  $I/Z$  pair presents a higher index towards the coast, and is the pair with the highest means and standard deviations,  $80.5 \pm 90.0$  (Figure 3 top centre). The  $Z/P$  pair presents a homogenous pattern, with the distinction of the western side of Downs, where the lowest index is found (Figure 3 top right). This last pair has a mean of  $77.1 \pm 30.5$ .

In regard to the multiple  $r^2$  of the linear model (Equation 3, Figure 3 mid section), the  $I/P$  pair shows that the relationship between the *Overlap* and the *Recruitment* of herring had an irregular pattern throughout the whole region, ranging from 12.7 to 33.8% (Figure 3 mid left). The  $I/Z$  pair presents stronger differences across the region barriers, thus distinguishing the Orkney-Shetland, Buchan, Banks, and Downs regions very well, where the  $r^2$  is lowest in the Banks region and towards the English Channel (Figure 3 mid centre). Overall, the  $r^2$  ranged from 12.7 to 29.6% for the pair  $I/Z$ . The  $Z/P$  pair presents stronger relationships overall, and the  $r^2$  ranged from 10.9 to 29.2% (Figure 3 mid right). The significance patterns (Figure 3 bottom) show similar patterns to those of  $r^2$ , with the  $p$ -value being lower in the regions with the strongest  $r^2$  yet providing evidence that the relationship between the *Overlap* and the *Recruitment* of herring is significant over the whole study region with exceptions in the Downs region.

When assessing the statistically significant relationships between the *Overlap* of each pair with the *Recruitment* of *C. harengus* (0 wr, Figure 4), on average, all pairs present a  $r^2$  between 10.85 and 33.85% ( $p$ -value  $\leq 0.05$ , Figure 3). The average *Overlap* of each predator-prey pair explains 23, 21, and 26% ( $I/P$ ,  $I/Z$ , and  $Z/P$ , respectively) of herring *Recruitment* (0 wr,  $p$ -value  $\leq 0.05$ , Supplementary Figure S4). When considered together, the overlaps of the three pairs explain 23% of the herring recruitment (Figure 4). The relationship between the three overlaps and the herring recruitment are on average negative, that is, as the overlap between the three trophic



**Figure 3.** *Overlap* indices (top, log-scale), multiple  $r^2$  (mid), and  $p$ -value (bottom) for the relationships between *Recruitment* (0 wr, 1-year-old NSAS herring) and the *Overlap* indices for each pair of predator/prey. Black polygons represent the following regions, from north to south, as in Payne (2010): Orkney-Shetland, Buchan, Banks, and Downs.

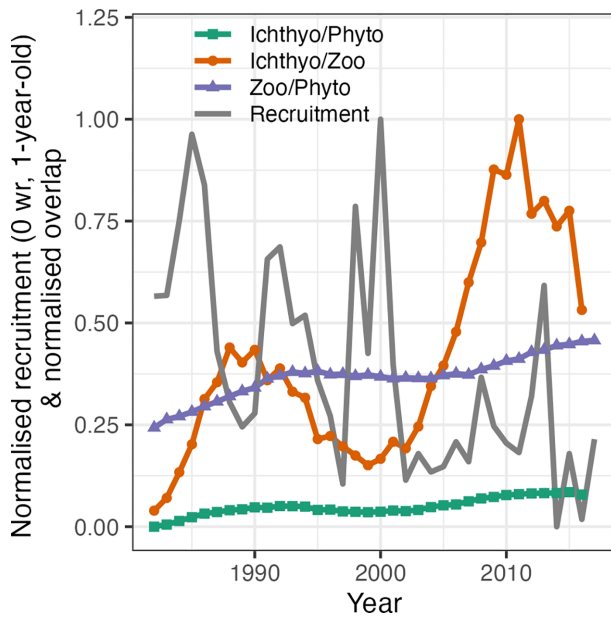
levels increases throughout the time-series, the recruitment decreases.

## Discussion

The objective of this study was to understand how the predator-prey spatio-temporal overlap at different trophic levels of the food chain explains the variation in pelagic fish populations. We found that (H1) the predator-prey overlap explains up to 23% of herring recruitment at 0 wr (Supplementary Figures S4 and S3), (H2) there is a spatial pattern in the overlap (Figure 3 top), and (H3) there is a spatial pattern in the relationship between the overlap and recruitment (Figure 3 mid and bottom). For the first time, we show that MMH dynamics explain al-

most a quarter of the recruitment variability of NSAS herring.

The environment plays an important role in fish recruitment, perhaps even more important than spawning-stock biomass alone (Payne *et al.*, 2009). Within the environmental factors, even though predator-prey dynamics have been used to predict recruitment (Alvarez-Fernandez *et al.*, 2015), our results show the importance of measuring relevant predator-prey pairs to make useful recruitment models, since the overlap of each of the three pairs explains recruitment at different trophic levels: *I/P*, *I/Z*, and *Z/P* (23, 21, and 26%, respectively). Our methodology is also applicable to the recruitment dynamics of other species, regions, and trophic levels. In the present study, given that the explanatory power was similar between each predator-prey pair (the percentages shown above), we confirmed the possibility of using



**Figure 4.** Normalized recruitment of NS herring (NSH, *C. harengus*, 0 wr, 1-year-old, grey) and normalized overlap for each pair of predator/prey (I/P, green; I/Z, orange; and Z/P, purple) for the regions with a statistically significant relationship between recruitment and overlap. “wr” stands for winter growth rings, which correspond to 1-year-old NSAS herring.

any trophic level regarding the NSAS herring for predicting recruitment.

The relationships between the spatio-temporal overlap of three trophic levels and the NSAS herring recruitment at 0 wr all resulted in negative correlations (Figure 4), which contradict the tenets of the MMH (Hjort, 1914; Cushing, 1990; Durant *et al.*, 2013). We consider three potential study constraints that may explain this contradiction: (i) feeding constraints: the prey field we used is not mechanistically relevant to this fish stock, and/or the first-feeders may not be the limiting stage; (ii) food-unrelated constraints: other factors unrelated to food may be more relevant to NS herring recruitment; and (iii) spatio-temporal constraints: the spatio-temporal resolution of the data is inadequate, or simply not representative of the NS.

### Feeding constraints

A negative relationship between NSAS herring and the overlap of the larvae with their prey may mean that, when the larvae are synchronized with their prey, their mortality is increased. A reason for this counter-intuitive result could be that some of the favourite prey of larval NS herring have not been included in the analysis, and/or that the analysis includes one or more species that are not preferred prey and for which abundance is negatively correlated to that of preferred prey. Previous studies suggest that the species we used for the zooplankton indices are part of the NS herring’s preferred prey taxa for the studied size classes (Supplementary Figure S1, Lusseau *et al.*, 2014; Alvarez-Fernandez *et al.*, 2015; Denis *et al.*, 2016). However, these studies have focused on either locations or time frames that may not be representative of those considered in the present study. In addition, prey selection partly depends on local environmental conditions (Wilson *et al.*, 2018), and larvae may even be characterized by mixed nutrition when transitioning from endogenous to exogenous feeding (Ma *et*

*al.*, 2012). Furthermore, the list of potential prey species of NS herring may comprise more taxa than those previously reported under limited spatio-temporal context. Nevertheless, including an upper length threshold and/or using *C. finmarchicus* as a prey item would have no impact on our results, as the larval sizes our data focus on do not prey on *C. finmarchicus* (Wilson *et al.*, 2018). However, having a better understanding of the variability of larval herring diet composition may prove relevant to the scope of potential environmental conditions across the NS.

The lower trophic level (phytoplankton) was represented by the Phytoplankton Colour Index (PCI) from the CPR survey. However, the PCI only represents the phytoplankton biomass (Edwards *et al.*, 2001; Batten *et al.*, 2003; Leterme *et al.*, 2005), and information on species composition is not included. A more realistic approach would be to more precisely characterize the phytoplankton trophic level for the NS herring’s trophic chain.

### Food-unrelated constraints

Spawning stock biomass has been reported to predict between 5 and 15% of the variance in recruitment (for 211 fish stocks, Cury *et al.*, 2014), which confirms how low the predictive power of stock-recruitment relationship is in marine fish populations (Cury *et al.*, 2014; Brosset *et al.*, 2020). As pointed out by Munch *et al.* (2018), the predictability of fish recruitment varies across taxa and improves with the number of sampled generations. Therefore, recruitment models need to integrate environmental conditions, parental effects, and species interactions in fisheries stock assessment and management (Cury *et al.*, 2014).

In the present study, we used a simplified version of the complex NS ecosystem (Gislason, 1994). Accounting for more complexity would potentially produce a positive relationship between the spatio-temporal overlap of three trophic levels with herring larvae and the NSAS herring recruitment (0 wr, Figure 3). However, by focusing on a P-Z-I trophic chain, we get an insight on the complexity of the NS ecosystem. In addition, a high overlap between herring larvae and their predators and/or competitors may lead to an increased mortality on herring before they reach recruitment, thus producing a negative relationship between the above-mentioned overlap and the NS herring recruitment. Notwithstanding, our findings may confirm that we are in the presence of a more complex ecosystem than the one considered here. For instance, a high overlap between zooplankton and phytoplankton may indicate that zooplankton would be less vulnerable to predation by fish. Therefore, obtaining more information on NS herring predators and competitors is necessary to disentangle a more complete overview of the NS herring ecosystem.

### Spatio-temporal constraints

Larval NS herring prey species may vary with location, time, and size. Illing *et al.* (2018) showed a strong positive relationship between NS herring larvae and the abundance of their prey. However, Illing *et al.* (2018) did not account for the spatial component of how MMH dynamics affects recruitment. In the present study, we show that there is a spatial pattern in the way predators and prey interact; both directly, as the degree to which they match in time depends on whether or not they match in space; and indirectly, as the degree to which they match in time, even if they also match in space, depends

on their location, as spatial variability in other environmental variables influences their likelihood of encounter (Durant *et al.*, 2007). Therefore, the negative relationship we have found in this study may be linked to spatial variability in the MMH dynamics for NS herring.

The high overlap between NS herring and their prey may also mean that the larvae are not moving and thus may not reach the areas with the most favourable growing conditions further in life (Sinclair & Tremblay, 1984; Durant *et al.*, 2021). Therefore, the ability of the larvae to move to more favourable conditions for the juvenile stage will also be limiting their survival (Peck *et al.*, 2012), and could thus explain in part why our results show a negative relationship between predator-prey overlap and recruitment. One solution would be to couple our approach to drift modelling (Romagnoni *et al.*, 2015; Romagnoni *et al.*, 2020; Vikebø *et al.*, 2021; Endo *et al.*, 2022). However, such an approach is computationally intensive and requires highly spatio-temporal data as to not inflate the error term (Ferreira *et al.*, 2014; Ferreira *et al.*, 2020). Here we addressed this limitation by using a modelling approach with inherent associated error.

There is a debate on whether or not the four spawning components of the NSAS herring stock (Orkney-Shetland, Buchan, Banks, and Downs) should be considered separately (Payne, 2010; ICES, 2021). The same debate should perhaps be considered when looking at recruitment dynamics as we did in the present study since the four spawning components identified have separate spawning grounds, migration routes, and nursery areas, even though they mix during the summer months (Payne, 2010). That is why the “state-space” assessment model (SAM) approach has been used for NSAS herring—it allows ready customization to the peculiarities of the stock (ICES, 2021), including its spatial constraints.

It has been shown that the timing of life history events (e.g. spawning, larval feeding) is linked to temperature on a larger scale (Durant *et al.*, 2005; Koeller *et al.*, 2009; Neuheimer *et al.*, 2018). In regard to time constraints in our study, an overlap between fish larvae and zooplankton could be essential for NS spring-spawning larvae as zooplankton abundance is high starting in May, while an overlap with phytoplankton could be important for NSAS larvae as zooplankton is low after October (Figure 2). In our study, we focused on the NSAS herring, therefore we would expect that the relationship with phytoplankton would play a more important role. However, that was not the case, possibly due to the fact the PCI is not representative of the succession of phytoplankton species of importance for larval herring.

Even if the data, methodology, and hypothesis have passed all the tests, such as the ones we presented above, MMH may just not be applicable everywhere, as is evident in the broken link between fish larvae and their food reported for both Pacific and Atlantic pelagic fish (Brosset *et al.*, 2020; Laurel *et al.*, 2021; Endo *et al.*, 2022). Furthermore, even MMH explains the survival around the critical period, the number of larvae at this stage may have no influence at the recruitment stage (Stige *et al.*, 2013).

## Conclusions

Based on the framework of the MMH, we showed that the overlap in both space and time with immediate lower trophic levels (i.e. small copepods and phytoplankton) explained 23% of the historical NSAS herring recruitment. We showed that

our predator-prey overlap metric is applicable in multiple systems, its performance remained similar across the NS trophic chain, and, more importantly, its predictive power increases the forecast horizon for identifying recruitment variations of NS herring, especially in the face of future temperature increases (Cury *et al.*, 2008; Ockendon *et al.*, 2014; Durant *et al.*, 2019). The unexpected negative correlation observed between recruitment and the spatio-temporal predator-prey overlap indicates that further research is required to fully understand the mechanisms responsible for recruitment variability in NS herring. Our results highlight the need for increased focus on the spatial variability in recruitment, multispecies approach, as well as considering other possible limiting stages (Munch *et al.*, 2018; ICES, 2021), factors (e.g. predation, competition, and physical environment), and metrics.

## Supplementary Material

Supplementary material is available at the ICESJMS online version of the manuscript.

## Conflicts of interest

There are no conflicts of interest.

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## Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

## Author contributions

A.S.A.F. developed the main idea in correspondence with A.B.N. and J.M.D. A.S.A.F. performed the analyses and the writing. A.B.N. and J.M.D. provided knowledge and expertise on the analyses, and helped with the modelling and the writing.

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