Mapping habitats for the suitability of jellyfish blooms around the UK and Ireland

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Abstract

There is increasing focus on the frequency of jellyfish blooms in the Northeast Atlantic because of negative interactions with humans. However, uncertainty exists as to whether perceptions of increasing bloom frequencies reflect reality due to limitations within long-term population trend data. This study therefore developed and applied a semi-quantitative mapping approach to visualise bloom suitability based on the physiological tolerance of seven jellyfish to ocean temperature, salinity, and a prey index across the Northeast Atlantic. A 10% increase and a 10% decrease in the environmental parameters was then applied to the maps to assess model sensitivity and the potential influence of environmental change on bloom suitability. The study found that optimal physiological temperatures and salinities combined with peaks in prey abundance drove higher bloom suitability and determined distribution. Several locations predicted to be at high risk of bloom occurrence off British and Irish coasts were found to coincide with areas of high anthropogenic activity that could be impacted by blooms. In the absence of long-term datasets on jellyfish population dynamics, the results and methods developed in this study allow an understanding of historic bloom events and predictions of future populations that will be useful in informing monitoring and management.

Key words: Habitat suitability mapping, GIS, Northeast Atlantic, UK and Ireland, Jellyfish blooms, Environmental change

Introduction

Several Scyphozoa, Ctenophora and Hydrozoa medusae taxa (hereafter, referred to as jellyfish) can occur in high numbers causing bloom events (Purcell et al., 2007; Richardson et al., 2009). Jellyfish blooms are perceived to be becoming more common globally, reflected by an increase in coverage within the media and scientific literature (Condon et al., 2012). However, debate exists as to the cause of bloom events and whether the perceived increase is reflective of actual conditions. Furthermore, few long-term datasets on jellyfish population abundance exist to corroborate perceptions (Condon et al., 2012; Sanz-Martín et al., 2016; Pitt et al., 2018). There is a need to better understand current bloom suitability and changes under future environmental scenarios. This is particularly important in coastal areas where blooms coincide with anthropogenic activities such as fishing, aquaculture and tourism, as well as industries that use seawater for cooling such as power generation, due to the detrimental economic and social impacts associated with such events.

Though limited, there is evidence to suggest that bloom events are increasing in the Northeast Atlantic (NEA) (Licandro et al., 2010; Palmieri et al., 2015). This is based in part, on increased detections of gelatinous material in annual Continuous Plankton Recorder (CPR) surveys since the early 2000s (Licandro et al., 2010) as well as a synchronous increase in the abundance of shelf and oceanic jellyfish species detected within the last decade (Gibbons and Richardson, 2008). However, this relatively short-term increase could be attributed to the natural long-term population cycles of certain species (Licandro et al., 2010). Within the NEA, intense blooming events have recently been reported off the coasts of the UK and Ireland (Doyle et al., 2008; Licandro et al., 2010; Painting et al., 2014), covering several subareas within the Food and Agriculture Organisation (FAO) major fishing area 27 (see Fig. 1) (hereafter defined as area 27). For example, *Pelagia noctiluca* blooms have recently occurred in the Porcupine and Rockall area of the NEA, which included Irish coastal shelf waters in 2007 (Doyle et al., 2008), and the interannual variation of jellyfish populations that occurs across the North and Irish Seas which includes blooms of *Cyanea capillata*, *Aurelia aurita an Chrysaora hysoscella* (Lynam et al., 2004, 2005).

Although historical blooming events occur in the area (Fraser, 1955), there is a widespread perception that jellyfish numbers are increasing, which could impact anthropogenic activities if these populations bloom more frequently (Palmieri et al., 2015). However, it is also possible that the perceived increase in bloom events is a result of increases in the marine footprint of coastal industries and the subsequent increase in the likelihood of negative interactions occurring with existing jellyfish populations (Duarte et al., 2013). More generally, the perceived increases could also be the result of reporting bias attributed to increased attention on blooming events as they are a significant ecosystem change. Despite the NEA being one of the most studied regions in terms of jellyfish populations and their ecology, there is still uncertainty surrounding their abundance over time, their broad distribution patterns and how these blooms vary (Lynam et al., 2004; Doyle et al., 2007; Lucas et al., 2012).

One way to improve this uncertainty is to consider spatiotemporal variation in environmental factors to improve understanding of bloom suitability in time and space, and how this may change in the future. As long-term population datasets on jellyfish species in the NEA has limitations, additional methodologies are needed to further understand medusae populations and the factors that influences their distributions. Habitat suitability mapping can be used to assess how environmental factors may influence spatiotemporal variation in jellyfish suitability through multicriteria evaluation of biotic and abiotic factors (Store & Kangas, 2001) thought to influence medusae numbers. For example, Collingridge et al., (2014) assessed the suitability of the temperature, salinity, and prey availability in the North Sea for the potential establishment of the invasive Ctenophore *Mnemiopsis leidyi* using a spatial mapping approach. Such approaches based on the suitability of study species to known environmental conditions allow for predictions of the distribution of gelatinous organisms to be made which could include the suitability of an area for jellyfish blooms. Spatial mapping approaches can therefore support mitigation efforts of potential impacts in locations visualised to be more suitable for blooms. The influence of changes to environmental parameters on a species can also be incorporated into models to estimate how overall suitability could change under different climate scenarios and the potential impact on coastal communities.

Temperature (Holst et al., 2012; Purcell et al., 2012; Pascual et al., 2014), salinity (Holst & Jarms, 2010; Purcell et al., 2007) and prey availability (Lilley et al., 2015) are known to increase survival and reproduction rates of jellyfish found in the NEA during their life cycle (Purcell et al., 2012; Collingridge et al., 2014) and are considered key drivers of blooming events of species that may require monitoring. Based on these environmental factors, this study aims to develop and apply a spatial mapping approach to assess the spatiotemporal suitability for jellyfish blooms within area 27. Identified taxa included in mapping scenarios include native and seasonal species that are known to bloom. As limitations exists in long-term population trend data, it is hoped that the outputs from this study will help inform future surveillance and mitigation measures of blooms in the region.

Methods

Mapping area

The extent of the present study was defined by subareas within the FAO major fishing area 27 that cover British and Irish coastlines. The subareas selected for bloom assessment were the North Sea (subareas 27.4a-c), the Irish

Sea and English Channel (subareas 27.7a-k) and the northwest coast of Scotland and Northern Ireland (subarea 27.6a) (Fig. 1).

Data Collection and Display

In the present study, only the abiotic (sea surface temperature, salinity) and biotic (prey abundance) factors affecting the final medusae phase of the life cycle were considered. In the NEA, this life cycle stage generally occurs during mid-year peaks (Gibbons and Richardson, 2008), so the main output displayed in this study relate to the summer (June-August) for each species. Although it is acknowledged that other life cycle stages will impact the formation of blooms (Holst & Jarms, 2010; Purcell, 2011; Holst, 2012), species and life cycle specific thresholds are largely unknown and could not be included in this study. For example, polyp populations, strobilation success and ephyrae survival rates have been linked to favourable environmental conditions for some species, contributing to increased recruitment that can lead to blooms of adult medusae (Holst & Jarms, 2010; Purcell, 2011; Holst, 2012).

NetCDF files were obtained for sea surface temperature (SST) and salinity (PPT) from the Met Office Hadley centre EN4.2.0 ocean series (Good et al., 2013). The NetCDFs represented monthly (from daily averages) SST in degrees centigrade (°C) (converted from kelvin) and salinity in parts per thousand (PPT) for the years 2000-2019. These years were chosen as a representation of a present-day time-slice of average conditions that jellyfish currently experience within area 27 (Fig. 1). The NetCDFs were converted into raster data sets (1º latitude X 1º longitude grid resolution) and displayed in ArcMap 10.5 using the WGS84 coordinate system. The monthly data layers were then averaged and visualised according to season (winter = December to February, spring = March to May, summer = June to August and autumn = September to November). The final SST and PPT data within the relevant subareas of area 27 (Fig. 1) were then extracted, focussing on the summer averages (See Online Resource 1, Fig. S1).

Data representing monthly average prey abundance was obtained from the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) Continuous Plankton Recorder (CPR) database from the year 2000 to 2012 (SAHFOS, 2016). Although a restricted subset of years within the present-day time-slice occurred due to data availability at the time of research, the CPR data set acted as the only spatial representation of a known jellyfish prey item for the region. Total eye count zooplankton larger than 2 mm were specifically selected as a prey proxy for jellyfish medusae within the CPR data as these organisms have been reported in the stomachs of jellyfish (Lilley et al., 2009). It is acknowledged that other planktonic organisms of a smaller sizes are an important prey item to some species, particularly at different life cycle stages and that medusae are also known to consume other organisms such as tintinnids and fish larvae (Hansson et al., 2005; Javidpour et al., 2016). However, thresholds relating to additional prey items and different life cycle stages could not be sourced for each species, so the data selected within the CPR layers was defined as a prey index that gives an indication of suitability for adult medusae.

The point data from the database that fell within the FAO subareas (Fig. 1) were selected and plotted based on sample longitude and latitude (in decimal degrees) in ArcMap. Each series of seasonal points was converted to grid cell layers that estimated plankton levels across the mapping area using ordinary kriging interpolations (Li & Heap, 2011), with the plankton eye counts set as the z-scores. The interpolation was based on Tobler's first law of geography that states that "everything is related to everything else, but near things are more related than distant things" (Sui, 2004, pg. 269). A spherical semi-variogram model was applied to the kriging interpolation, using the squared differences between z-scores to identify when autocorrelation no longer occurred between samples (Li & Heap, 2011). The annual seasonal raster data layers based on the interpolation were averaged to produce present-day average prey index data layers, consistent with the SST and PPT NetCDFs (Fig. S1).

Species Selection and Threshold Assignment

Study species were chosen based on known ranges and physiological tolerances to ocean temperature, salinity, and the prey index available in the literature. Species included in the study are *Aurelia aurita, Chrysaora hysoscella, Cyanea capillata, Cyanea lamarckii, Pelagia noctiluca* and *Rhizostoma octopus.* These are known to bloom and are native to the UK and Irish waters. The siphonophore *Physalia physalis* was also included in the study because until recently it was considered to be an occasional visitor and is an example of a species that could increase in the NEA due to climate change (Hinder et al., 2012). Recent *P. physalis* outbreaks in the Celtic Sea Shelf have been attributed to wind acting as drift pathway into area 27 from more southernly latitudes (Headlam et al., 2020). Increased storminess because of climate change (Hinder et al., 2012) could result in increased numbers of *P. physalis* moving into the area. Therefore, an understanding of present-day suitability and how it could change in the region is required for this economically disruptive species.

For each species, environmental thresholds in relation to each of the biotic and abiotic parameters were derived from the scientific literature, using the following google scholar searches: ‘species’ AND ‘environmental parameter’ AND ‘threshold’ (e.g. “’*Aurelia aurita*’ AND ‘ocean temperature’ AND ‘survival’). On occasions where no species thresholds were found, data from the Ocean Biogeographical Information System (OBIS) library of species population occurrence and associated oceanographic conditions were used.

Searches produced little information relating to species-specific prey requirements. Species were therefore categorised according to the size of medusae (small and large) as there is evidence that the level of prey consumed is correlated to medusae size (Purcell, 2003; Rosa et al., 2013; Lilley et al., 2015). This enabled suitability thresholds to be assigned for the two medusae groups where species specific data was lacking. It was assumed that by using this methodology, some variation in prey requirements would be represented, as greater prey clearance rates within food webs have been associated with larger medusae (Graham and Kroutil, 2001; Purcell, 2003). The small jellyfish group was defined as medusae with a diameter of 20 cm and under and the large species were defined as having a medusae diameter larger than 20 cm. Medusae sizes stated in the Marine Life Information Network (MarLIN) species list descriptions were used to place each species into the large or small groups. Species that were classed as large medusa were, *C. capillata, C. hysoscella* and *R. octopus* and the species classed as small medusae were *A. aurita, P. noctiluca, C. lamarckii* and *P. physalis*. However, it must be acknowledged that this does not account for ontogenetic changes in the types and amount of prey consumed by jellyfish species over the course of their life cycle (Graham and Kroutil, 2001; Fleming et al., 2015), which could not be accounted for in this study due to the lack of life cycle specific thresholds available.

Development of Semi-Quantitative Spatial Maps

Semi-quantitative habitat suitability maps were developed by reclassifying the average present-day seasonal data layers according to the physiological thresholds collected for each species (Fig. 2a-c) , considering the range of temperatures where survival, reproduction and blooms can occur (Fig. S2). Grid cells within the environmental raster data layers were then given a suitability ranking based on physiological thresholds for each abiotic and biotic parameter: ‘0’, below survival threshold; ‘1’, above survival but below reproduction thresholds; ‘2’, above reproduction but below bloom threshold; ‘3’, above bloom threshold (Fig. 2b). This was repeated for the ‘spring’, ‘summer’, ‘autumn’ and ‘winter’ environmental conditions, but a focus was given to the conditions in summer representing the NEA mid-year peak and this data was displayed (Fig. 3). The three corresponding reclassifications of the SST, PPT and prey index data layers for each season were then overlaid and suitability at each raster square was assigned using minimum cell statistics (Fig. 2c-f). The lowest reclassification score within the overlay was displayed in the final map as it was assumed to be the limiting factor because of the impact on jellyfish suitability.

Validation

To validate the scoring methodology, environmental data layers were reclassified to assess if the methodology could represent a historic and well reported bloom event and conditions in the years leading up to, during and after the event. *P. noctiluca* bloom events occurred in 2007 and 2008 within the coordinates 45º N to 58º N and 1º W to 26º W, with reports indicating an increase in cnidaria occurrence in the CPR surveys in the area since 2002 (Licandro et al., (2010). Data layers for SST, PPT and the prey index representing the average mid-year conditions from the year 2002-2006 within the stated coordinates were extracted from the average present-day environmental data layers. The resultant data layers were reclassified based on the *P. noctiluca* physiological threshold range. Reclassified layers were overlaid and average suitability scores for each raster square were calculated over the time-period. The process was repeated for the average mid-year conditions for the years 2007 and 2008 when the outbreaks of *P. noctiluca* were reported, and also for the years 2009-2012 to represent the average suitability at the end of the time period that data was available for. The average suitability scores at the start of the time period were compared with the average suitability scores at the end of the time period to see if an increase in suitability rankings matched the increases in occurrence reported in the CPR records. The 2007 and 2008 average suitability scores were then compared with the two data sets representing non bloom years to see if higher bloom suitability was ranked during the known bloom years.

For the other species mapped in the study, an additional literature search (Lynam et al., 2004; Doyle et al., 2008; Painting et al., 2014; Bastian et al., 2011a; Bastian et al., 2011b) was conducted of their known present-day distributions within area 27 of the NEA (Fig. 1), including instances where blooms have been known to occur. Species occurrence records for each sub-are reported in the literature were compared with the average present-day suitability scores obtained using the mapping methodology to assess accuracy of the mapping approach in terms of jellyfish suitability and their spatial distributions.

Map Sensitivity

For each species, an evaluation was carried out of how varying the environmental parameters affected the sensitivity of model outputs. This was used to simulate generic changes to the environment and assess the subsequent effect on bloom suitability across the FAO subareas based on the sensitivity shown within the maps. Values within the SST, PPT and prey index data layers were increased and decreased by 10%, with data layers subsequently reclassified based on species thresholds and then overlaid. The percentage change in the highest suitability scores of grid cells was compared to the initial present-day reclassifications.

Results

Present-day Thresholds and Suitability

The physiological threshold ranges (ranges of each environmental parameter where varying levels of suitability was stated) for each species based on the initial literature review are displayed in Table 1. Generally, as the environmental parameters increased, so did the suitability rankings of cells. This was the case for both temperature and the prey index thresholds. The exception was the two *Cyanea* species that were more suited to colder temperatures than the other species. All species were able to survive, reproduce and bloom in marine waters in terms of salinity (< 35 ppt), with tolerance varying little between species.

Based on the literature derived species thresholds (Table 1) and the reclassifications of the present-day environmental data layers (Fig. S2), blooming was predicted to be possible for five of the jellyfish species (*A. aurita, P. noctiluca, C. capillata, C. lamarckii* and *C. hysoscella*), with populations of the other two species capable of reproducing (*R. octopus* and *P. physalis*) at certain times within the year (Table 2). However species-specific physiological tolerances resulted in seasonal and spatial variation in environmental suitability for medusae and the ability for populations to bloom. Four of the seven species (*A. aurita, P. noctiluca, R. octopus,* and *P. physalis*) were predicted to have the highest frequency of “reproduce” and “bloom” rankings across the subareas during the summer, indicating that higher mid-year temperatures were generally associated with blooms (Table 2). For the two *Cyanea* species, bloom events were predicted to be more likely during spring, however, greater levels of reproduction suitability were attributed to *C. capillata* for the summer than for *C. lamarckii* and highest suitability for *C. hysoscella* was in autumn (Table 2).

Generally, bloom rankings occurred more frequently for the smaller scyphomedusae (e.g. *A. aurita*) compared to the larger species (e.g. *R. octopus*) (Fig. 3). Waters within the northern and southern Celtic Sea and to the southwest of Ireland (subareas 27.7h, 27.7g and 27.7j respectively) were predicted to be most suited to blooms of *A. aurita,* and *P. noctiluca*. These southwestern subareas were also predicted to be most suitable for the three species that had no present-day bloom rankings (locations where "reproduce" rankings occurred for *R. octopus*, *C. hysoscella* and *P. physalis*). In terms of the spatial distribution of *C. capillat*a and *C. lamarckii,* the North Sea was the most suitable region (subarea 27.4), specifically the northern North Sea (subarea 27.4a). However, for some species, areas within the map were not suitable, achieving a "below survival" ranking, despite being predicted as the most suitable time of the year overall. For example, subarea 27.7a achieved below survival rankings for *R. octopus*, *C. hysoscella*, and *C. capillata* despite neighbouring subareas achieving the highest suitability rankings for these species (e.g. subarea 27.g).

Reclassifications of the data layers representing the SST, PPT and prey index from 2002-2012 within the coordinates 45º N to 58º N and 1º W to 26º W resulted in general agreement with the patterns of *P. noctiluca* samples that occurred within the CPR data that was reported by Licandro et al., (2010) (Table 3). Negligible areas of below survival rankings (between 1.75 and 2.25% of the area) occurred over the 10-year averages of the data layers. When comparing the earlier years within the time period (2002-2006), with the later years (2009-2012), average suitability was greater during the more recent years (49.17% "reproduce" and "bloom" rankings compared to 38.51%) (Table 3), indicating that the higher suitability scores do coincide with increasing medusae occurrence recorded by the CPR. The average suitability score for *P. noctiluca* within the 2007 and 2008 average data layers (years when blooms of *P. noctiluca* were reported within the coordinates) was the highest overall (62.72% of raster squares achieving a reproduce or bloom ranking), which included the greatest frequency of bloom rankings (Table 3). The scoring methodology was therefore deemed to be able to roughly determine when conditions within area 27 were suitable for blooms to occur and capture changes in suitability over time when compared to actual records of a species of medusae, despite the exact geographic distributions of suitability not matching actual records.

Sensitivity Analysis

Sensitivity analysis was used to determine the influence that changes in environmental factors would have on the suitability for each species (Fig. 4). Increasing temperature by 10% (Fig. 4a) generally resulted in the greatest predicted suitability increases for the larger scyphomedusae (*R. octopus* 23% “reproduce” and *C. hysoscella* 16% “reproduce” increase) that had initially showed relatively low suitability across the mapping site compared to the smaller scyphomedusae. Increased temperature suitability for the smaller medusae was also predicted (*A. aurita* 5% “bloom”, *P. noctiluca* 5% “bloom” and *P. physalis* 18% “reproduce” increase), but the increases were proportionally lower than for the large medusae, as larger areas of highest suitability were already predicted to be possible under present-day conditions (Fig. 3). The species associated with colder temperatures were predicted to increase in terms of bloom suitability in response to the decreased temperatures (both *C. capillata* and *C. lamarckii* 64% “reproduce” increase). The increase in PPT resulted in little predicted suitability change for all species, but the decrease was predicted to result in larger decreases (between 5% and 11% for all species) in suitability across the mapped regions (Fig. 4b).

The percentage changes in maximum suitability in relation to the prey index change revealed greater sensitivity within the mapping output compared to the impacts of changing the SST and PPT layers (Fig. 4c). A positive association of jellyfish suitability occurred in response to changes in prey availability by the large medusae and small medusae groups, but for larger medusae, proportionally greater changes were predicted. For example, *C. capillata, R. octopus* and *C. hysoscella* (20%, 22% and 19% increase in maximum suitability respectively) were predicted to show greater increases in highest suitability rankings than the more common and smaller *A. aurita* and *P. noctiluca* medusae (5% and 17% increase respectively). Only *P. physalis* was more sensitive in response to temperature where all other species where most sensitive to changes in the prey index data layers.

When overlaying the SST, PPT and prey index sensitivity reclassification (Table 4), the 10% increases were predicted to lead to increases in overall suitability rankings for five species. This included large increases (95%+) in the number of cells being ranked with the highest suitability scores during the summer for *A. aurita*, *P. noctiluca*, *P. physalis* (all “bloom” rankings), *C. hysoscella* and *R. octopus* (“reproduce” rankings). Overall bloom rankings for the two *Cyanea* species were the only occasions when an overall decrease in suitability was measured in responses to the 10% increases in the environmental data layers, due to the negative impact of increasing temperatures (Fig. 4a). Conversely, when the 10% decreases to the environmental reclassifications were overlaid, there was a 95-100% decreases in the most suitable rankings that were predicted for each species, including the two *Cyanea* species, despite the more suitable temperatures.

Discussion

Jellyfish blooming events are reported to potentially be increasing in the NEA; however, corroboration of such trends is challenging due to limitations and gaps within long-term population monitoring datasets (Condon et al., 2012). Given the potential socio-economic impacts of bloom events, the ability to accurately predict them would be greatly beneficial in informing monitoring and mitigation efforts.

In the present study, habitat suitability mapping was completed for seven bloom forming jellyfish species found in UK and Irish waters, providing new insights into how key environmental factors may contribute towards current and future spatiotemporal trends in bloom occurrence. Based on average environmental data layers and literature derived species thresholds, habitat suitability maps were generated to reflect present-day species occurrence that provide a means to understand how these populations may respond to environmental change. The relatively simplistic approach was able to give a general overview of suitability and bloom risk for a greater number of species and for a wider geographic area than more complex hydrodynamic suitability models of gelatinous medusae that exists within area 27 (e.g. Collingridge et al., 2014).

Present-day Jellyfish Populations

Comparison of the present-day suitability maps generated in this study with reported occurrence records for jellyfish medusae indicated that whilst the methodology gave a good overview of suitability for certain species, for others suitability predictions did not match reported present-day distributions. For example, regions to the southwest of the maps (subareas 27.7e, 27.7f and 27.7g, including parts of the Celtic Sea) where highest suitability was determined are known to contain populations of *A. aurita, C. hysoscella, P. noctiluca, and P. physalis* medusae (Doyle et al., 2008; Licandro et al., 2010; Doyle et al., 2013; OBIS, 2020). This was also the case for more northern and north-eastern areas (subareas 27.4a, 27.4b and 27.6a) where populations of *C. capillata, C. lamarckii, P. noctiluca* and *A. aurita* have previously been sampled in high numbers (Lynam et al., 2004; Painting et al., 2014). However, there were examples where ‘below survival’ was projected for some species in areas where medusae are known to occur (Doyle et al., 2013; Fleming et al., 2015). For example, within in subarea 27.7a there are a number of coastal embayments such as Carmarthen and Tremadoc Bay, the Solway Firth and Rosslare Bay where *R. octopus* is known to occur (Doyle et al., 2013) that the maps ranked as unsuitable. Also, species such as *R. octopus, A. aurita* and *C. hysoscella* that are constrained to coastal environments by a benthic stage within their life cycle (Doyle et al., 2007; Doyle et al., 2008) had similar (and in some cases higher) suitability projections for areas further out to sea, which does not match with their known distributions. *R. octopus* is only recorded in coastal waters (Bastian et al., 2011a), not out into the Celtic Sea where increased suitability was predicted. Both *C. capillata* and *C. lamarckii* have a benthic stage, but have been recorded out into the North Sea (Painting et al., 2014) and the Irish Sea (Bastian et al., 2011a) matching the distribution of the present-day suitability projections of medusae in this study. However, suitability was not projected in the maps across the whole of these areas (*C. capillata* ranked as "below survival" to the southeast of subarea 27.4b and all of 27.7a) where samples of these species have been recorded (Painting et al., 2014). The occasions where jellyfish suitability in this study and their known distributions do not match is likely due to data gaps in the environmental data layers and species threshold ranges which are discussed in the limitations

Validation indicated that the methodology could distinguish bloom years from non-bloom years within the time-slices that the maps represent using the *P. noctiluca* blooms in the Celtic Sea in 2007 and 2008 as an example. *P. noctiluca* is not constrained by a benthic phase and increased suitability was measured further out to sea, including areas where it is known to occur which included large areas projected to be suitable for blooms (Licandro et al., 2020). However, the increased bloom suitability projected for *P. noctiluca* in the Celtic Sea during this study are further south of where the species is mostly reported, which includes the bloom events in waters to the Northwest of Ireland (Doyle et al., 2008; Bastian et al., 2011b).

Potential Changes in Bloom Suitability

The variation in jellyfish suitability in response to the sensitivity analysis allows for some conclusions to be drawn as to whether blooms could increase in the study region. The changes in ocean temperature and prey abundance in the present study were predicted to significantly influence bloom suitability, with increases resulting in increasing suitability overall. The predictions suggest that future spikes in jellyfish abundance, within the naturally occurring long-term cyclical patterns (Condon et al., 2013), could occur in areas that are currently suitable for reproduction, if temperatures were to rise (or remain suitable) and prey abundance increases, especially within the seasons that are currently most suitable. The conclusions drawn from the outputs in this study agree with the results of lab-based studies that highlight the importance of temperature and prey abundance for the suitability of common scyphozoa linking increases to blooms (e.g. Wang & Li, 2015).

Such environmental conditions do occur in the NEA, which is experiencing rapid increases in water temperatures (Philippart et al., 2011) and plankton blooms attributed to increasing coastal eutrophication and industrial runoff (Cartensen et al., 2001; Almroth & Skogen, 2010; Condon et al., 2013). Projections for the NEA suggest that in some areas 2°C increases in sea surface temperatures are possible by the end of this century (Philippart et al., 2011), which is similar to the increases applied to the temperature layers in the current study during the sensitivity analysis, suggesting increased bloom suitability is possible. No projections were found that suggest future temperatures, salinity and prey abundance will decrease across the region, suggesting future bloom suitability relating to the species studied are unlikely to reduce.

If bloom events increase in response to environmental change, there is potential for a rise in detrimental socioeconomic impacts to occur (Graham et al., 2003; Palmieri et al., 2014) such as disruption of coastal tourism activity (Graham et al., 2003; Purcell et al., 2007; Ghermandi et al., 2015) increased mortality in aquaculture finfish (Purcell et al., 2007; Doyle et al., 2008) and increased interference with coastal fishery operations (Knowler, 2005; Palmieri et al., 2014). For example, high numbers of marine finfish (mainly salmon) aquaculture producers are situated across the Northern Irish and Scottish west coasts (particularly within subareas 27.6a and 27.4a), which were predicted by this study to be at high bloom suitability for stinging species such as *P. noctiluca* and *C. lamarckii*. High economic losses and mortalities of farmed salmon were attributed to the *P. noctiluca* blooming events of 2007 off the Irish coasts (Doyle et al., 2008), and further such events could have significant implications on the industry. The bloom suitable regions for a range of species to the south west of the maps (subareas sub areas 27.7h, 27.7g and 27.7j) and adjacent coasts coincide with locations associated with high levels of coastal tourism, which includes Devon and Cornwall. The areas predicted to be of high bloom suitability in the North Sea and to the Southwest of the UK and Ireland, also coincide with the fishing locations of large capture fishing fleets (MMO, 2018). Both tourism and fisheries have been impacted by annual blooming events of the study species in other geographic locations (Purcell et al., 2007), including the annual disruption to tourism by *P. noctiluca* in the Mediterranean (Ghermandi et al., 2015) and added cost of bloom bycatch experienced by fisheries in the Adriatic (Palmieri et al., 2015). The potential impact on these industries in the NEA has been acknowledged, but quantification of how impacts will compare with areas that currently experience higher bloom frequencies are unknown (Palmieri et al., 2015). The results of this study could therefore be used to identify locations of potential socioeconomic impact of blooms due to conflict with anthrophonic activity.

Limitations and future development

Several limitations to the mapping approach taken in this study require acknowledgement. Jellyfish are a relatively understudied group in terms of their environmental requirements, and it is possible that the thresholds ranges do not fully represent the adaptability and plasticity of each species. For example, *C. capillata* is known to occur further south (Painting et al., 2014) than the temperature suitability distributions suggest in this study (Fig. S2a), There were also instances where it was not possible to obtain species-specific suitability thresholds, particularly in relation to prey requirements and there are additional factors known to influence blooms which could not be included due to the lack of data that exists. Such data gaps included dispersal of medusae by ocean currents, pH, oxygenation, additional prey items as well as how each species undergo ontogenetic shifts in relation to their environmental requirements throughout their life cycle (Condon et al., 2001; Richardson et al., 2009, Purcell 2012). This likely led to instances where suitability was underestimated, such as the below survival predictions for *R. octopus* in subareas 27.7a in locations where it is known to regularly occur in coastal bays.

There were also occasions where species showed high suitability in subareas adjacent to subareas of low suitability, which is unrealistic due the lack of physical barriers within the marine environment. A possible cause is data gaps within the environmental data layers. Specifically, within the CPR data, large areas within the NEA are not sampled, resulting in prey index suitability rankings being based on fewer samples. Some subareas (e.g. area 27.7a) therefore likely contained underestimations of suitability for certain species (Online resource 1, Fig. S2c). Conversely, areas such as the Celtic sea that are sampled more frequently by the CPR tows showed greater suitability for *P. noctiluca* compared to the Norwest of Ireland (where comparatively fewer CPR samples are taken) where it is more widely reported (Doyle et al., 2008). If detailed data are collected in relation to the prey requirements of different jellyfish (such as more spatial distribution information that also captures the variety of prey items consumed and species-specific threshold ranges), improvements will be made in how the methodology projects suitability distributions.

There is also an absence of polyps and ephyrae distribution data for these species in the NEA (Bastian et al., 2011a), so the relationship between the suitability for potential medusae populations and the other life cycle constraints requires further study. The methodology currently only captures suitability in relation to the medusae phase of the life cycle. Polyp recruitment, strobilation success and ephyrae survival rates have been linked to favourable temperature increases, salinity levels and prey abundances which vary from the medusae

(Holst & Jarms, 2010; Purcell, 2011; Holst, 2012). If the locations of polyp populations can be located for species constrained to coastal areas such as *A. aurita*, the modelling could be applied to assess the contribution of polyp populations, strobilation success and ephyrae survival towards bloom formation, particularly if life cycle specific thresholds can be sourced and the environmental data are reclassified during the season when each life cycle phase is known to happen in the NEA.

However, despite these limitations the models are still able to give a general overview of medusae suitability across area 27 (Fig. 1), replicate known historical bloom events and suggests how changes in certain environmental factors may influence future populations of medusae. The relatively simple methods and data requirements allow much broader applications compared to more complex hydrodynamic modelling that are often constrained to few species and restricted geographic ranges (e.g. Collingridge et al., 2014). The overall suitability of the NEA generated in this study can be used to identify relevant case studies of locations where suitability and future bloom risk could be assessed in more detail using higher resolution and more region species assessment of jellyfish suitability.

Conclusions

This study demonstrates that habitat suitability mapping is a valuable tool in helping to predict spatiotemporal trends in bloom suitability under different environmental scenarios, supporting the development of monitoring programmes and strategies to help mitigate socio-economic impacts. However, there is a need to improve data collection and transfer between biological information and modelling approaches to overcome the challenges presented by blooms of jellyfish medusae (Fleming et al., 2015). Despite the identified limitations and data gaps, the methodology provides valuable insight into the distribution of jellyfish bloom suitability across a large geographic area where reports of blooms are increasing that can enable potential impacts in the NEA to be identified. The methods applied in this study could easily be adapted to other species, different life cycle stages and locations if the correct environmental data and species threshold ranges can be sourced to identify where potential bloom impact could occur. The identification of spatial patterns of the likelihood of blooming events can feed into the prioritisation of monitoring and be used to develop risk-based mitigations strategies such as anti-jellyfish nets on beaches used for recreation that coincide with greater bloom suitability. Although effective management for marine pest species poses a complex challenge due to the high level of connectivity in marine systems (Tidbury et al., 2016), it may be possible to enable sectors at risk to implement preventative measures in bloom-prone regions.

Table 1 Environmental condition threshold rangess where survival, reproduction and blooms were possible according to physiological tolerances by species as derived from the literature

Environmental Condition Thresholds						
Species	**SST (˚C)**	**Refs**	**PPT**	**Refs**	**Prey Index**	**Refs**
Aurelia aurita	Survival: 5-12 Reproduce: 13-14 Bloom: 15+	Lucas, 2001; Holst, 2012; Purcell et al., 2012; Pascual et al., 2014; Lilley et al., 2015, OBIS, 2020	Survival: 17-29 Reproduce: 30-34 Bloom: 35+	Purcell, 1984; Lucas, 2001; Holst & Jarms, 2012; OBIS, 2020	Survival: 5-39 Reproduce: 40-59 Bloom: 60+	Morand, 1987; Lilley et al., 2015
Pelagia noctiluca	Survival: 5-11 Reproduce: 12-14 Bloom: 15+	Avian, 1986; OBIS, 2020	Survival: 30 Reproduce: 31-34 Bloom: 35+	Doyle et al., 2008; Rosa et al., 2013; OBIS, 2020	Survival: 5-39 Reproduce: 40-59 Bloom: 60+	Purcell, 1984; Rosa et al., 2013; Lilley et al., 2009; Lilley et al., 2015
Cyanea capillata	Survival: 16 Reproduce: 11-15 Bloom: 10	OBIS, 2020	Survival: 25-31 Reproduce: 32-34 Bloom: 35+	Holst & Jarms, 2010; Holst, 2012; OBIS, 2020	Survival: 30-59 Reproduce: 60-99 Bloom: 100+	Fancett, 1988; Brewer, 1989; Purcell, 2003
Rhizostoma octopus.	Survival: 14 Reproduce: 15 Bloom: 16-20	Lilley et al., 2009; Fuentes et al., 2011; OBIS, 2020	Survival: 30-33 Reproduce: 34 Bloom: 35+	Purcell et al., 2012; Fuentes et al., 2011; OBIS, 2020	Survival: 40-59 Reproduce: 60-99 Bloom: 100+	Fancett, 1988; Lilley et al., 2009; Fuentes et al., 2011
Chrysaora hysoscella	Survival: 13-14 Reproduce: 15 Bloom: 16+	Sparks, 2001; Purcell et al., 2012	Survival: 20-31 Reproduce: 32-34 Bloom: 35+	Holst & Jarms, 2012	Survival: 30-59 Reproduce: 60-99 Bloom: 100+	Flynn & Gibbons, 2007; Lilley et al., 2015
Cyanea lamarckii	Survival: 16 Reproduce: 11-15 Bloom: 10	Lucas, 2001; Purcell et al., 2012	Survival: 25-31 Reproduce: 32-34 Bloom: 35+	Lucas, 2001; Holst & Jarms, 2010; Holst, 2012	Survival: 15-39 Reproduce: 40-59 Bloom: 60+	Brewer, 1989; Lilley et al., 2015
Physalia physalis	Survival: 2-14 Reproduce: 15-19 Bloom: 20+	Birsa et al., 2010; OBIS, 2020	Survival: 30 Reproduce: 31-34 Bloom: 35+	OBIS, 2020	Survival: 30-39 Reproduce: 40-59 Bloom: 60+	Fancett, 1988; Purcell, 2003

Table 2 Proportion (%) of cell rankings within the maps for each jellyfish medusae within the present-day time slice per season across the FAO subareas

Species	Suitability	Winter	Spring	Summer	Autumn
Aurelia aurita	Below Survival	8.72%	0.56%	0.00%	0.00%
	Survival	91.28%	98.87%	55.93%	82.11%
	Reproduce	0.00%	0.56%	37.29%	14.21%
	Bloom	0.00%	0.00%	6.78%	3.68%
Pelagia noctiluca	Below Survival	10.26%	2.82%	2.26%	1.58%
	Survival	88.21%	91.53%	48.02%	66.32%
	Reproduce	1.54%	5.65%	42.94%	28.42%
	Bloom	0.00%	0.00%	6.78%	3.68%
Cyanea lamarckii	Below Survival	51.79%	11.30%	35.59%	12.11%
	Survival	39.49%	41.24%	31.64%	61.58%
	Reproduce	6.15%	35.03%	32.77%	26.32%
	Bloom	2.56%	12.43%	0.00%	0.00%
Cyanea capillata	Below Survival	51.58%	87.69%	51.41%	35.59%
	Survival	40.00%	3.59%	25.99%	49.15%
	Reproduce	8.42%	6.15%	22.60%	14.69%
	Bloom	0.00%	2.56%	0.00%	0.56%
Rhizostoma octopus	Below Survival	100.00%	99.44%	71.19%	96.07%
	Survival	0.00%	0.56%	21.47%	3.93%
	Reproduce	0.00%	0.00%	7.34%	0.00%
	Bloom	0.00%	0.00%	0.00%	0.00%
Chrysaora hysoscella	Below Survival	100.00%	99.44%	39.52%	29.55%
	Survival	0.00%	0.56%	52.10%	41.48%
	Reproduce	0.00%	0.00%	8.38%	20.45%
	Bloom	0.00%	0.00%	0%	8.52%
Physalia physalis	Below Survival	89.01%	32.09%	31.92%	49.47%
	Survival	10.99%	65.78%	45.74%	41.06%
	Reproduce	0.00%	1.60%	21.28%	9.47%
	Bloom	0.00%	0.53%	1.06%	0.00%

Table 3 Average mid-year suitability scores for *P. noctiluca* within the coordinates 45º N to 58º N and 1º W to 26º W during time periods when increasing occurrences where being recorded (2002-12) and a period when outbreaks were reported (2007-8)

Time slice	**Below Survival**	**Survival**	**Reproduction**	**Bloom**
2002-2006	1.72%	59.77%	36.78%	1.74%
2007-2008	2.25%	35.03%	49.15%	13.56%
2009-2012	2.25%	48.58%	42.93%	6.21%

Table 4 Overall proportional (%) change in the highest cell suitability rankings for each species during the mid-year peak in response to the 10% sensitivities applied to the environmental data layers

Species	**Percentage change in highest overall suitability**	
	Plus 10% Sensitivity	**Minus 10% Sensitivity**
Aurelia aurita	242%	-100%
Pelagia noctiluca	242%	-100%
Cyanea lamarckii	-48%	-95%
Cyanea capillata	-40%	-100%
Rhizostoma octopus	200%	-100%
Chrysaora hysoscella	178%	-100%
Physalia physalis	95%	-100%

Figure legends

Fig. 1 Subareas off the British and Irish coasts within the FAO major fishing area 27 where jellyfish bloom suitability was assessed (subareas 27.4a-c, 27.6a and 27.7a-k)

Fig 2 Pictorial overview of the mapping methodology from the initial reclassification of environmental data layers to the final cell overlay. a) the initial environmental parameter to be reclassified, b) the physiological threshold ranges and suitability scores used to reclassify the environmental parameters, c) the reclassification of the environmental parameter, d) the temperature reclassification, e) the salinity reclassification, f) the prey index reclassification, g) the minimum cells statistics overlay of the 3 reclassified environmental parameters

Fig. 3 Predicted suitability rankings of UK and Irish waters to resident jellyfish species within the mid-year in terms of SST, PPT and the prey index layers

Fig. 4 Proportional (%) change in the highest suitability rankings within the maps in response to the +/-10% SST, PPT and the prey index changes for each species. Grey bars: 10% increase, Black bars: 10% decrease

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656 Figure 1

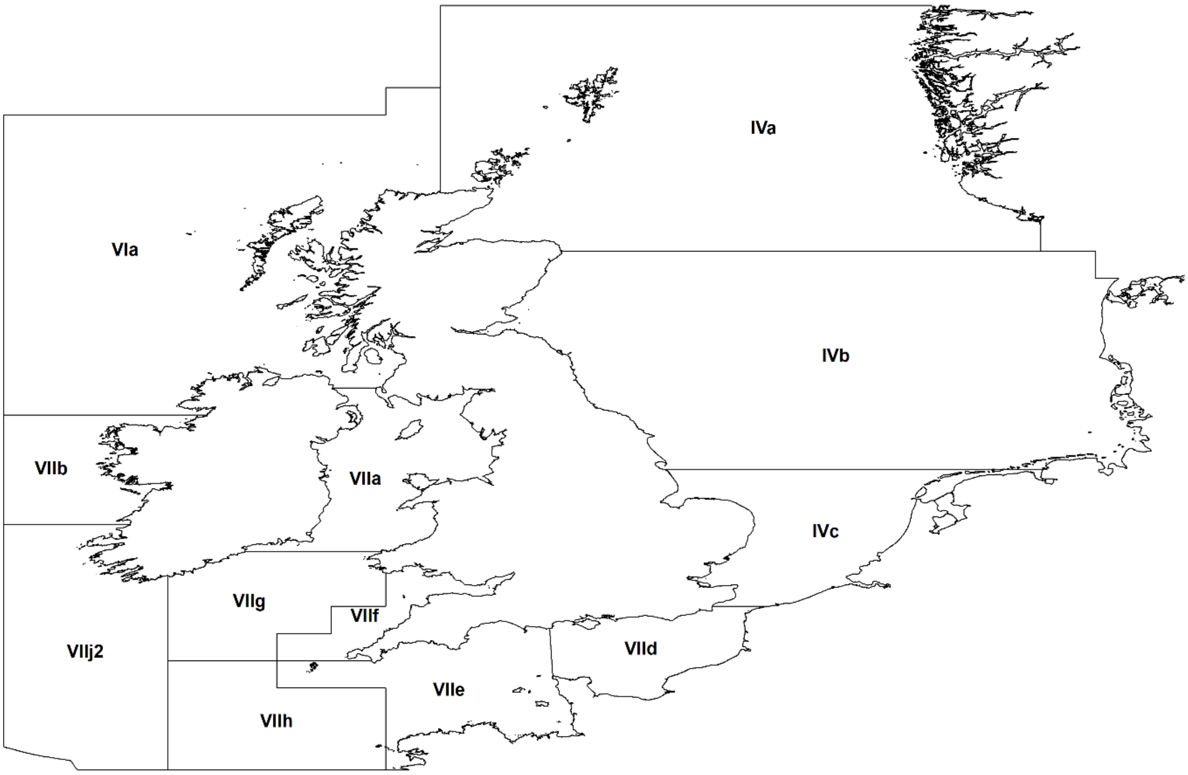
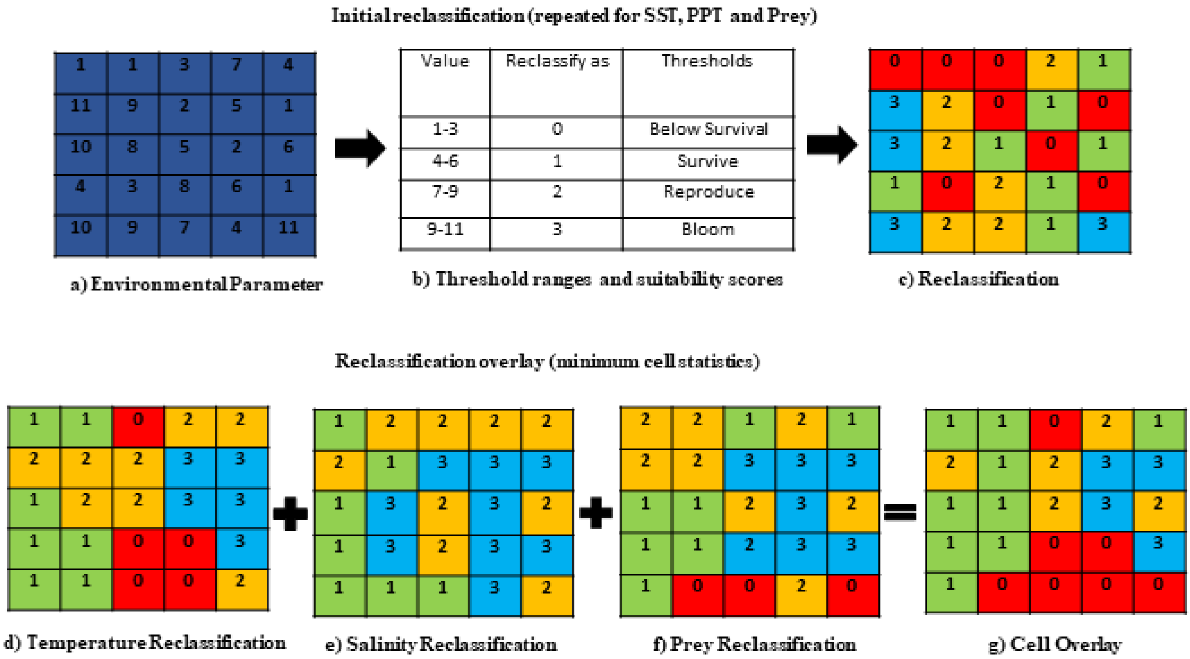


Figure 2



Initial reclassification (repeated for SST, PPT and Prey)

1	1	3	7	4
11	9	2	5	1
10	8	5	2	6
4	3	8	6	1
10	9	7	4	11

a) Environmental Parameter

Value	Reclassify as	Thresholds
1-3	0	Below Survival
4-6	1	Survive
7-9	2	Reproduce
9-11	3	Bloom

b) Threshold ranges and suitability scores

0	0	0	2	1
3	2	0	1	0
3	2	1	0	1
1	0	2	1	0
3	2	2	1	3

c) Reclassification

Reclassification overlay (minimum cell statistics)

1	1	0	2	2
2	2	2	3	3
1	2	2	3	3
1	1	0	0	3
1	1	0	0	2

d) Temperature Reclassification

1	2	2	2	2
2	1	3	3	3
1	3	2	3	2
1	3	2	3	3
1	1	1	3	2

e) Salinity Reclassification

2	2	1	2	1
2	2	3	3	3
1	1	2	3	2
1	1	2	3	3
1	0	0	2	0

f) Prey Reclassification

1	1	0	2	1
2	1	2	3	3
1	1	2	3	2
1	1	0	0	3
1	0	0	0	0

g) Cell Overlay

Figure 3

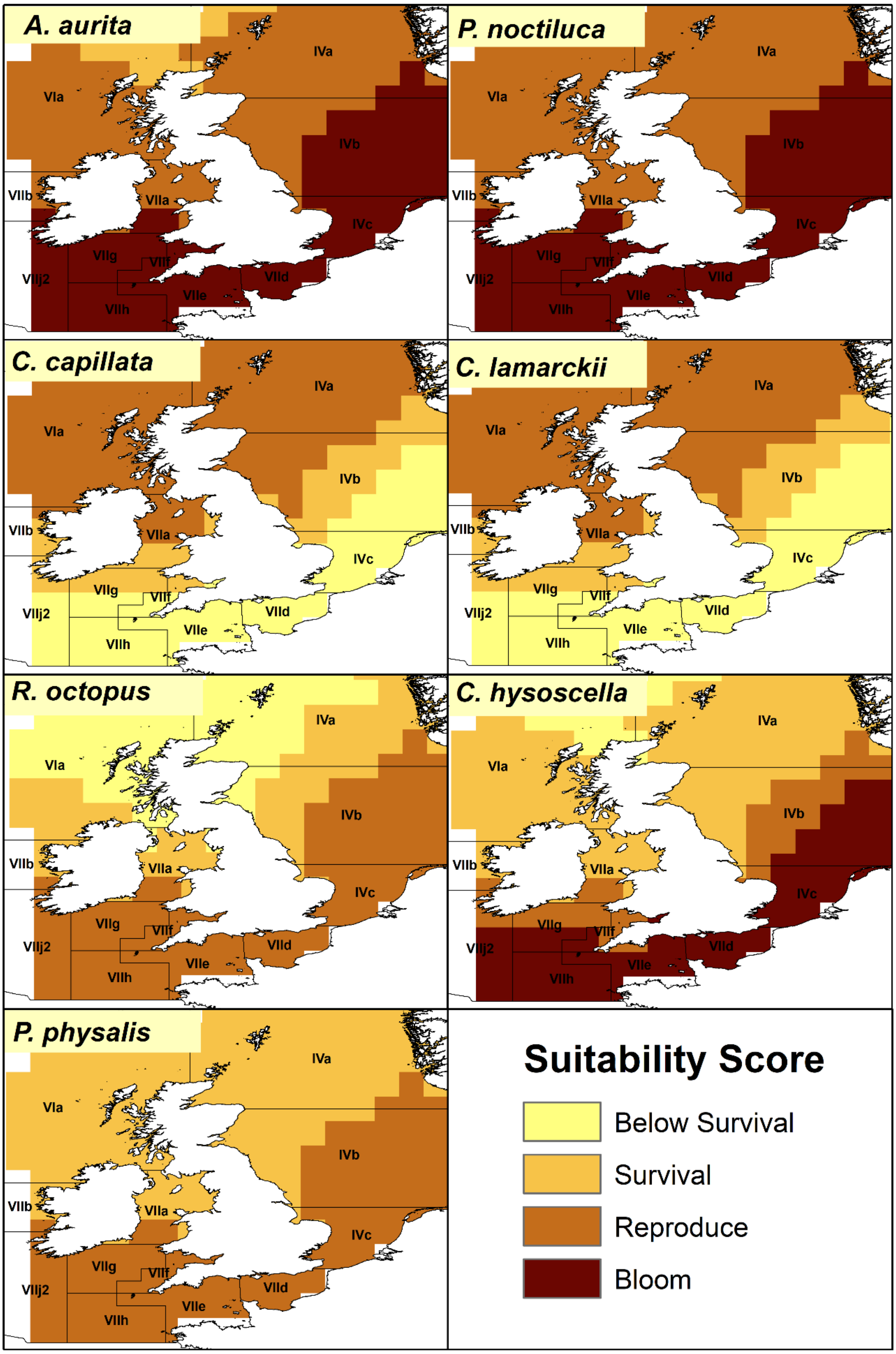

A. aurita
P. noctiluca
C. capillata
C. lamarckii
R. octopus
C. hysoscella
P. physalis
IVa
IVb
IVc
VIa
VIIa
VIIb
VIIg
VIIf
VIIj2
VIIh
VIIe
VIId
Suitability Score
Below Survival
Survival
Reproduce
Bloom

Fig 4a

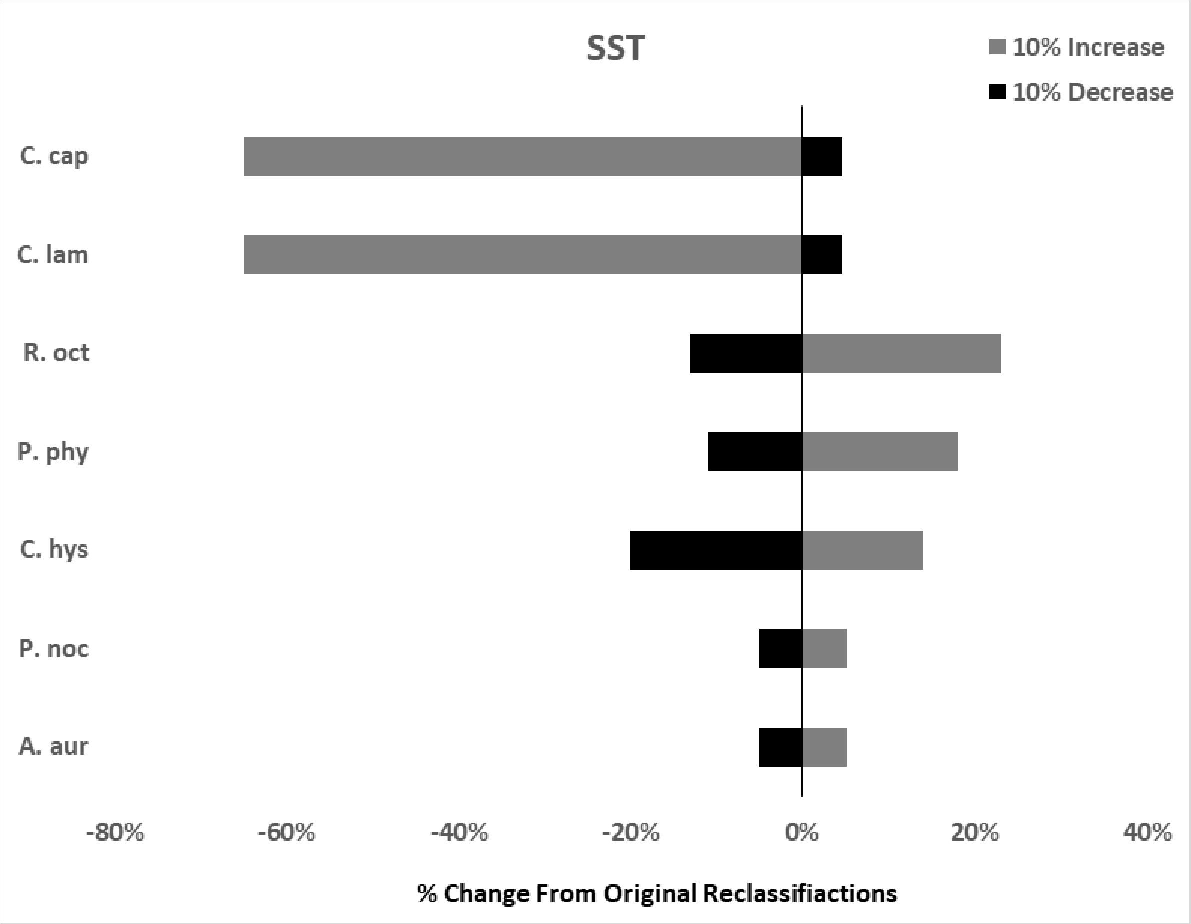

SST
10% Increase
10% Decrease
C. cap
C. lam
R. oct
P. phy
C. hys
P. noc
A. aur
-80%
-60%
-40%
-20%
0%
20%
40%
% Change From Original Reclassifiactions

Fig 4b

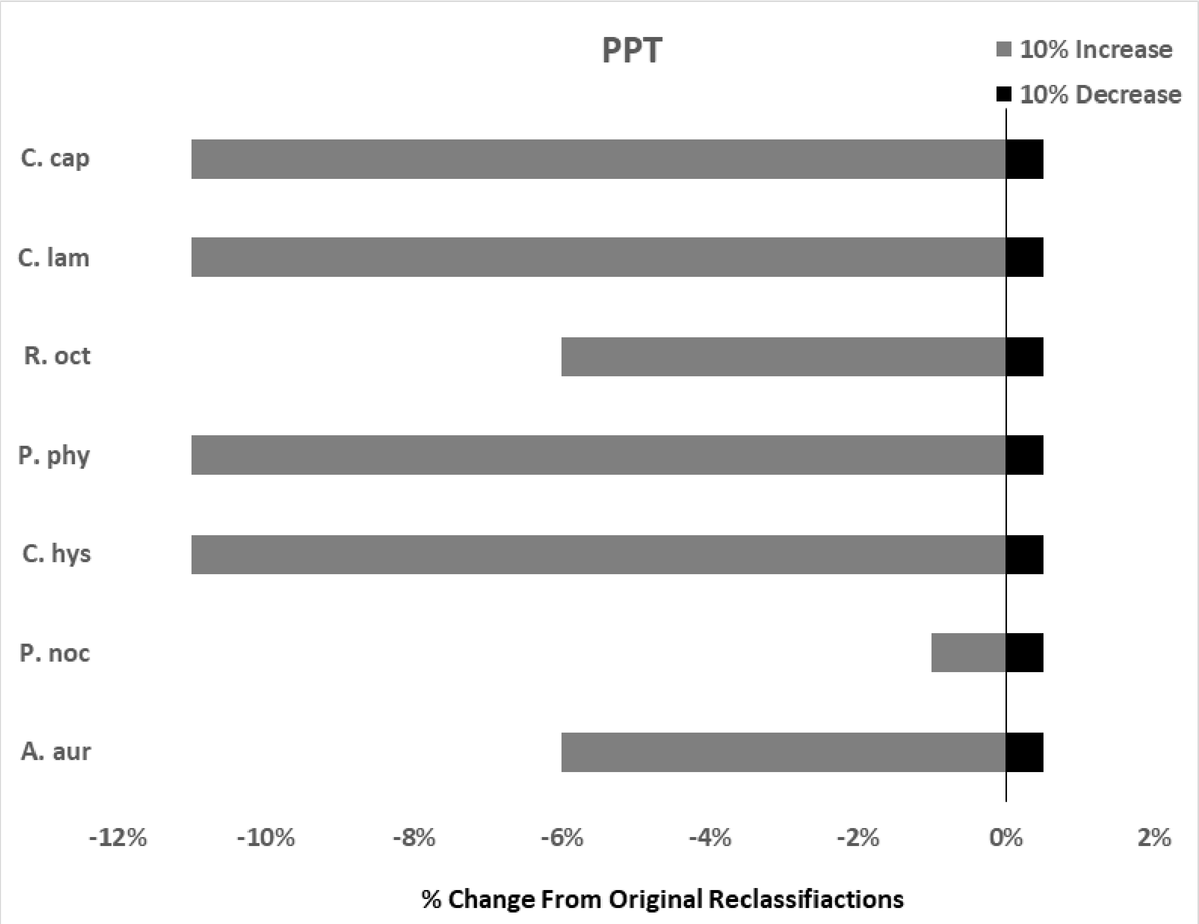
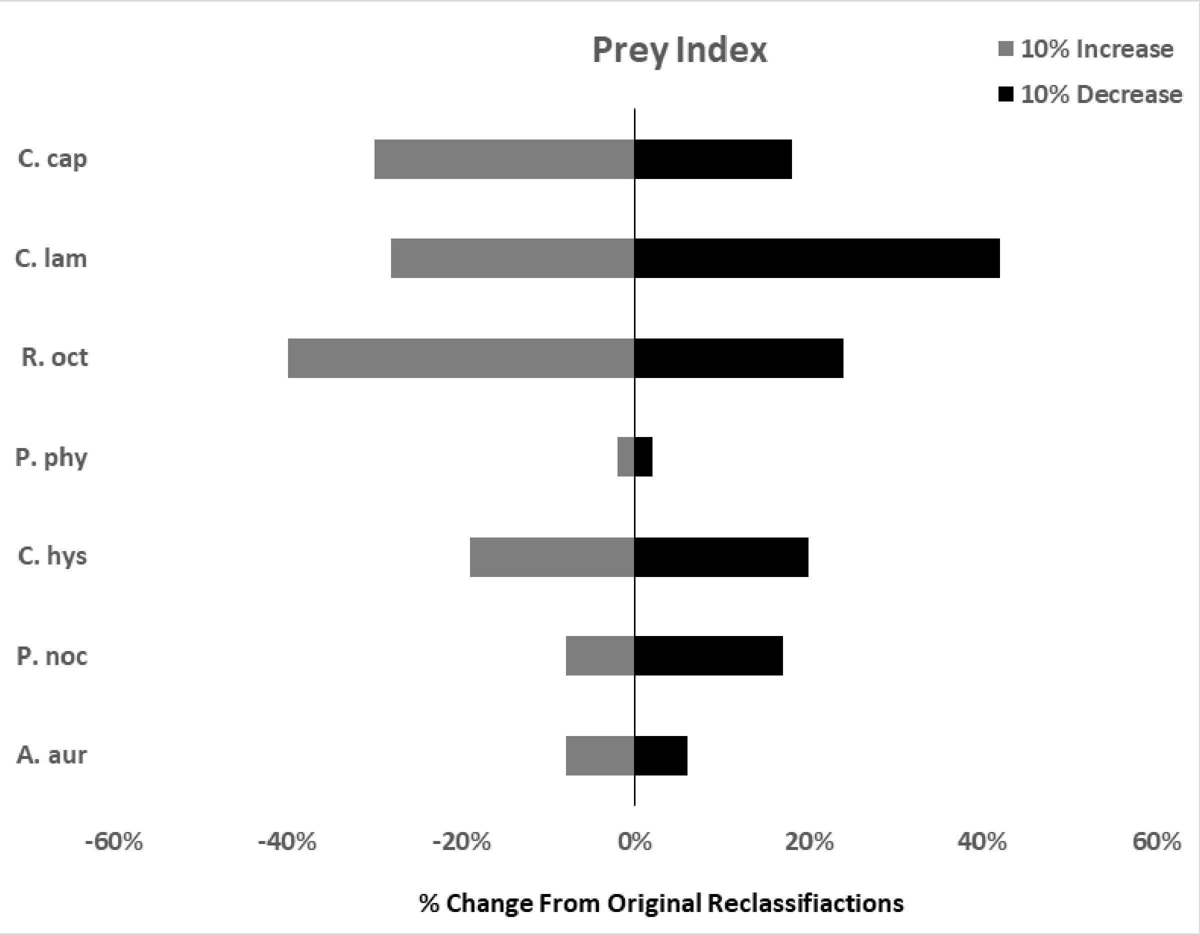

PPT
10% Increase
10% Decrease
C. cap
C. lam
R. oct
P. phy
C. hys
P. noc
A. aur
-12%
-10%
-8%
-6%
-4%
-2%
0%
2%
% Change From Original Reclassifiactions

Fig 4c


Prey Index
10% Increase
10% Decrease
C. cap
C. lam
R. oct
P. phy
C. hys
P. noc
A. aur
-60%
-40%
-20%
0%
20%
40%
60%
% Change From Original Reclassifiactions