

Large-scale environmental drivers of kelp biofouling

Victoria Delannoy^{1,2}, Maria Alguero-Muñiz¹, Eleni Christoforou^{1,3}, Yacob Haddou¹, Annabell Macphee¹, Keri McEachnie¹, Kyla Orr⁴, Sofie Spatharis¹✉

¹ School of Biodiversity One Health and Veterinary Medicine, University of Glasgow, Scotland

² UFR918 Terre, Environnement, Biodiversité, Sorbonne Université, Sorbonne University, France

³ Cyprus Marine and Maritime Institute, CMMI House, Vasileos Pavlou Square, 6023 Larnaca, Cyprus

⁴ KelpCrofters Ltd, Plockton, Highlands, Scotland, IV52 8TU.

✉ sofie.spatharis@glasgow.ac.uk

Abstract

Macroalgae are currently a focal point of research because of their essential contributions to coastal ecosystem dynamics, their ability to mitigate the effects of climate change, and their potential as an innovative and sustainable food source. Regarding wild macroalgae, epiphytic and invertebrate epibionts form important communities that enhance local biodiversity and ecosystem functioning. However, in farmed populations for commercial use, biofouling epibionts can severely impact macroalgae physiology, growth and yield impacting the quality of the product. Due to their ecosystem health importance and aquaculture industry impacts, an increasing number of longitudinal studies focused on specific locations, are trying to establish the drivers of macroalgae epibionts. However, to enable sufficient contrasts in environmental conditions and reveal macroecological patterns in epibiont occurrence, it is essential to compile data from multiple locations covering a wide geographical scale. To achieve this, here we analyze data on macroalgae and epibiont taxonomy, study location, and environmental conditions that we have compiled from a systematic literature review and from the Marine Copernicus and NASA OBPG databases of marine data. Our results show that 58.18% of studies on macroalgae epibionts are focused on the Northeast Atlantic coast, which is particularly relevant to understand the current expansion of seaweed aquaculture in this region. We found that bryozoan fouling depends on sea surface temperature (SST) and an increased biofouling risk was predicted for latitudes greater than 58° in the NE Atlantic coast and around coastal areas in Scotland with cold freshwater inflows. Other main biofouling taxa such as hydrozoans and gastropods showed a higher probability of occurring on

35 farmed or planted kelp as opposed to wild populations, although gastropods tended to be absent at salinities
36 lower than 30 psu. Our findings provide a first basis for understanding seaweed biofouling risks in the North-
37 East Atlantic ecoregion and can serve for spatial planning of the positioning of new seaweed farms.

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39 **Keywords:** biofouling risk, kelp, seaweed aquaculture, North-East Atlantic
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41 Introduction

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43 Macroalgae aquaculture is rapidly gaining popularity due to the benefits of derived products for human health
44 (Bizzaro et al., 2022), its positive effects on ecosystem health (Roleda and Hurd, 2019), its potential key
45 roles in reducing worldwide hunger (FAO, 2021; Jagtap and Meena, 2021) and in climate change
46 mitigation (Duarte et al., 2022, 2017). If properly exploited, seaweed farming represents a €9B opportunity
47 for Europe and could create 115,000 jobs over 10 years (Vincent et al., 2023). Despite the recognized suitability
48 of North-East Atlantic coasts for expansion of seaweed aquaculture (Macias et al., 2025), the seaweed farming
49 industry in the UK and Europe is mostly characterized by small farms producing 1-10 T seaweed (wet weight)
50 per year with limited use of technology. Although UK seaweed industry is on the cusp of scaling to commercial
51 profitability, a major limitation to the productivity in the mesotrophic waters of the northeast Atlantic is the
52 proliferation of biofouling organisms on out-planted seeded lines and cultivated seaweed (Rolin et al., 2017)
53 which can have unpredictable and devastating impacts on product yield and quality (Rolin et al., 2017; Visch
54 et al., 2020). Despite the clear benefits of macroalgae aquaculture for ecosystem health and human societies
55 and the damages incurred by biofouling to the industry, there is very limited knowledge on how the marine
56 environment is driving the presence of epibionts on macroalgae. Shedding more light on this topic is key to
57 predicting the well-being of coastal seaweed under future temperatures and seascapes as well as empowering
58 more sustainable and profitable seaweed aquaculture practices.

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60 In macroalgae, and specifically kelp aquaculture, hydrozoans are amongst the most problematic epibionts as
61 they are particularly resistant to physical removal and chemical treatment whereas their spread cannot be
62 controlled due to their ability to rapidly reproduce and regenerate (Bernard et al., 2019). Bryozoans are equally
63 problematic due to their capacity to encrust the seaweed in dense lace-like mats (Førde et al., 2016). Although
64 bryozoans and hydrozoans contribute disproportionately to biofouling biomass (Rolin et al., 2017), gastropods
65 and amphipods can also be particularly damaging due to direct grazing effects (Behera et al., 2022; Hansen et
66 al., 2006) and increased allergen risks (Motoyama et al., 2007). When biofouling invertebrates attach and
67 colonize the macroalgae surface, they interfere with photosynthesis, respiration and gas exchange by
68 physically blocking and shading the surface area of the blade. This alters the pH and oxygen concentration of
69 the surrounding water, leading to reduced growth and health of the surrounding population. The build-up of
70 epibionts also increases the weight and drag of the macroalgae, further impacting their ability to take up
71 nutrients via passive movement (Visch et al., 2020). Hydrozoans colonies are also associated with a decrease
72 of several key nutrients in the kelp such as copper, cadmium, nickel and chromium (Getachew et al., 2015).
73 Due to these effects, biofouling greatly reduces the health of farmed seaweed and leads to reduced crop yield,

74 product quality, market value, increased waste and human health risks (Bannister et al., 2019; Visch et al.,
75 2020).

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77 Latitudinal studies of epibiont monitoring over an annual cycle are important for understanding the succession
78 of biofouling species on wild or farmed macroalgae and thus regulating the timing of optimal macroalgae
79 harvesting times (Corrigan et al., 2023). Site-specific studies can also be useful for fine-scale adjustments
80 within existing farms such as horizontal and depth positioning of seeded lines (Khan et al., 2024). However,
81 latitudinal studies often lack sufficient information and contrasts in environmental conditions to empower
82 causal modelling of biofouling drivers. To overcome this limitation, data on macroalgae epibionts from
83 multiple published studies can be compiled with environmental data from open-source databases such as
84 Copernicus and NASA OBPG.

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86 The aim of the present study was thus to investigate the environmental drivers of macroalgal biofouling taxa
87 and their large-scale distribution patterns. To achieve this goal, we compiled data from a systematic literature
88 review of papers on macroalgae epibionts as well as from E.U. Copernicus Marine Service Information
89 (CMEMS), Marine Data Store (MDS) and NASA - OBPG. Specifically, we first aimed to identify specific areas
90 globally where macroalgae sampling efforts have been more intensive and specific macroalgae groups that
91 have received the highest attention. Focusing on kelp, we then identified the environmental variables that
92 were driving the presence of specific biofouling species. Finally, focusing on the North-East Atlantic region —
93 which represented the highest research effort— we modelled the spatial distribution of biofouling taxa on
94 kelp. Our findings represent the first milestone towards quantifying seaweed biofouling risk at a broad scale
95 and thus enabling spatial planning of new farm locations as well as predictions of biofouling risk under further
96 climate change scenarios.

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98 **Methods**

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100 Overview of methodological approach

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102 To address the study aims, we carried out the following steps. First, we compiled data on macroalgae epibionts
103 from a systematic literature review and we supplemented it with environmental data from the E.U. Copernicus
104 Marine Service Information (CMEMS), Marine Data Store (MDS) and the NASA Ocean Biology Processing Group.
105 Second, we identified geographical regions that have received increased research focus and thus sampling
106 effort on macroalgae epibiont communities. Third, using all compiled data, we modelled the relationship
107 between probability of occurrence of seaweed biofouling taxa in relation to environmental covariates. Finally,

108 we further supplemented environmental data from the North-East Atlantic region, which was identified in
109 step 2, and using the model developed in step 3, we modeled and graphed the spatial distribution of specific
110 biofouling taxa.

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112 Systematic literature review

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114 A systematic literature review of published papers on communities of epibionts on macroalgae was conducted
115 on Google Scholar, using the following keywords: “seaweed” OR “kelp” OR “macrofauna” + “epibionts” OR
116 “epifauna” OR “biofouling”. The search was initiated from the year 1976, when the oldest relevant publication
117 was recorded, until April 15th, 2023. This initial search resulted in 364 papers on macroalgae epibionts. A
118 further selection process took place whereby a set of criteria was applied based on the abstract, materials and
119 methods of each publication (Figure S1). An important criterion applied at this stage was the selection of
120 papers which focused on invertebrate communities of epibionts rather than a single epibiont species or
121 epiphytic algae. This approach was essential for addressing our objectives whereby the absence of an epibiont
122 implied that the species was absent or sufficiently rare rather than it was not investigated. This secondary
123 selection process resulted into 54 publications which corresponded to 234 sampling events: 112 samplings on
124 Kelp (Laminariales), 102 on other brown algae (other Ochrophyta), 16 on green algae (Chlorophyta) and 24 on
125 red algae (Rhodophyta). “Sampling event” does not completely overlap with “sampling site”, “algae species”,
126 and “sampling period”; e.g. multiple “sampling events” of the same “algae species” might take place within a
127 “sampling site”. After the full selection process, the oldest “sampling event” recorded in our dataset was in
128 1978 and the latest was in 2019. Finally, we supplemented the resulting dataset with our own monitoring of
129 a seaweed farm from the Island of Skye, NW Scotland that was collected between September 2021 to July
130 2022 (described in the Supplementary material).

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132 Data compilation

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134 For each of the 54 publications we extracted the seaweed species, epibiont taxon (at species level whenever
135 possible), season and year of sampling, and condition (wild vs not wild). We collected the GPS position of the
136 sampling site provided by the articles. In some cases, GPS position had to be deduced from the map provided
137 in the paper with a precision of <3 km, which was possible because all studies were conducted at small scales
138 of <50km. For each epibiont taxon, complementary information on higher taxonomic levels was extracted
139 from the World Register of Marine Species (WoRMS) with the ‘Taxon match tool’ function of the website.
140 Three epibionts observations out of 5794 were not recognized by WoRMS and were deleted from the dataset.
141 In many papers, in situ environmental data were either not measured, not provided or were measured with

non-comparable protocols. To ensure the availability of consistent environmental data for our analysis, we used satellite data to obtain sea surface temperature (SST), salinity, wave height and chlorophyll-a concentration for each sampling site. All data were obtained from Copernicus Marine data store or the earth data NASA website and represented the value at sea surface level (Table 1). Each sampling location was associated with a mean value of environmental data weighted by area at a 5 km radius buffer circle.

For each environmental covariate, a mean was calculated for each sampling location across time. Due to data availability, the local means of SST and chl-a were calculated from January 2003 to December 2019 and the local means of salinity and wave height were calculated from 1993 to 2019 (2019 being the last epibiont sampling event in our dataset). Data averaging was essential to a) minimize the effect of seasonal and interannual variation, b) obtain a more representative value of the general environmental conditions at each sampling location, and c) to ensure consistency as publications were often not defining the sampling season.

Table 1. Publicly available data sources where environmental variables were compiled from and that were used in the seaweed biofouling distribution models.

Variable (Unit)	Resolution	Years	Identifier	Reference
SST (°C)	0.042° (~4 km)	01-2003 12-2019	MODIS_AQUA_L3_SST_MID- IR_DAILY_4KM_NIGHTTIME_V2 019.0	NASA OBPG, 2020; DOI: 10.5067/MODAM-1D4N9
Salinity (psu)	0.083° (~8 km)	01-1993 12-2019	GLOBAL_MULTIYEAR_PHY_001_ 030	Global Ocean Physics Reanalysis; DOI: 10.48670/MOI-00021
Chl-a (mg.m ⁻³)	0.042° (~4 km)	01-2003 12-2019	AQUA MODIS Level-3 Binned Chlorophyll, Version 2022	NASA OBPG, 2022; DOI: 10.5067/AQUA/MODIS/L 3M/CHL/2022
Wave height (m)	0.2° (~22 km)	01-1993 12-2019	GLOBAL_MULTIYEAR_WAV_001 _032	Global Ocean Waves Reanalysis; DOI : 10.48670/MOI-00022

160 Data analysis

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162 To test which of the algal groups in our study (Laminariales, other Ochrophyta, Rhodophyta, Chlorophyta) are
163 richer in epibiont phyla we used two indicators of diversity and namely the phyla richness per sampling event
164 as well as the Whittaker index WI :

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$$WI = \frac{S}{\bar{a}} - 1 \text{ (Shmida and Wilson, 1985)}$$

166 where S is the total number of epibiont phyla recorded for a given algal group and \bar{a} is the average number of
167 distinct epibiont phyla per sampling event for the given algal group. The WI index is based on presence-
168 absence data thus making it more robust against sampling biases that affect abundance measures. The WI is
169 reflecting community turnover and thus offers complementary insights to phyla richness. Specifically, higher
170 WI values are expected for algal groups in which sampling events were more different to each other in terms
171 of their epibiont phyla composition. Essentially, WI values are reflecting the epibiont phyla turnover observed
172 via phyla accumulation curves which we calculated with 'specaccum function' from 'vegan' package (Oksanen
173 et al., 2024), using a randomization method of 1000 permutations.

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175 We fitted a binomial Generalized Mixed Effects model to estimate the probability of biofouling presence of
176 specific epibiont taxa on macroalgae fronds as a function of Macroalgae group (kelp vs other Ochrophyta),
177 kelp condition (wild vs not wild), SST, salinity, chl-a, and wave height. The publication identifier was included
178 as a random effect to account for differences in sampling protocols and effort as well as the fact that each
179 publication might have repeated measures across different algae species and sites. Each epibiont taxon was
180 treated as a binomial response (presence/absence) because abundance was often not recorded, or was
181 expressed in non-comparable units, and because studies often sampled different seasons which were pooled
182 together inducing bias on measures of epibiont biomass. Models were fitted with the 'glmer' function of the
183 lme4 package version 1.1-32 in R (Bates et al., 2015). We performed backward selection of important variables
184 using Likelihood Ratio Test. Using the model formula of epibionts probability presence as a function of
185 environmental variables and using spatial environmental layers, we were able to spatially predict the
186 probability of presence of Bryozoa and Cnidaria (phylum), Hydrozoa (Class), Gastropoda and Gymnolaemata
187 (Class), Littorinimorpha and Cheilostomatida (Order) and Ischyroceridae (Amphipod family) (Table 2). This
188 analysis was done using the 'predict' and 'st_rasterize' functions from the 'stats' and 'stars' packages
189 respectively (Pebesma and Bivand, 2023; R Core Team, 2024).

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191 Results

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193 Geographical distribution of studies on seaweed biofouling

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From a total of 55 studies (54 from the literature review + our own dataset), over half (58.18%) took place in the North Atlantic whereas much less took place in the South Atlantic Ocean (5.45%). From the remaining studies, 18.18% took place in the Pacific Ocean, 7.27% in the Arctic Ocean, 5.45% in the Mediterranean Sea, 3.64% in the Indian Ocean and 1.82% in the Antarctic Ocean. Sampling effort varied across algae groups: a total of 11 species of Laminariales (kelp), 38 species of other Ochrophyta, 12 species of Rhodophyta, and only 4 species of Chlorophyta were focal species of macroalgae.

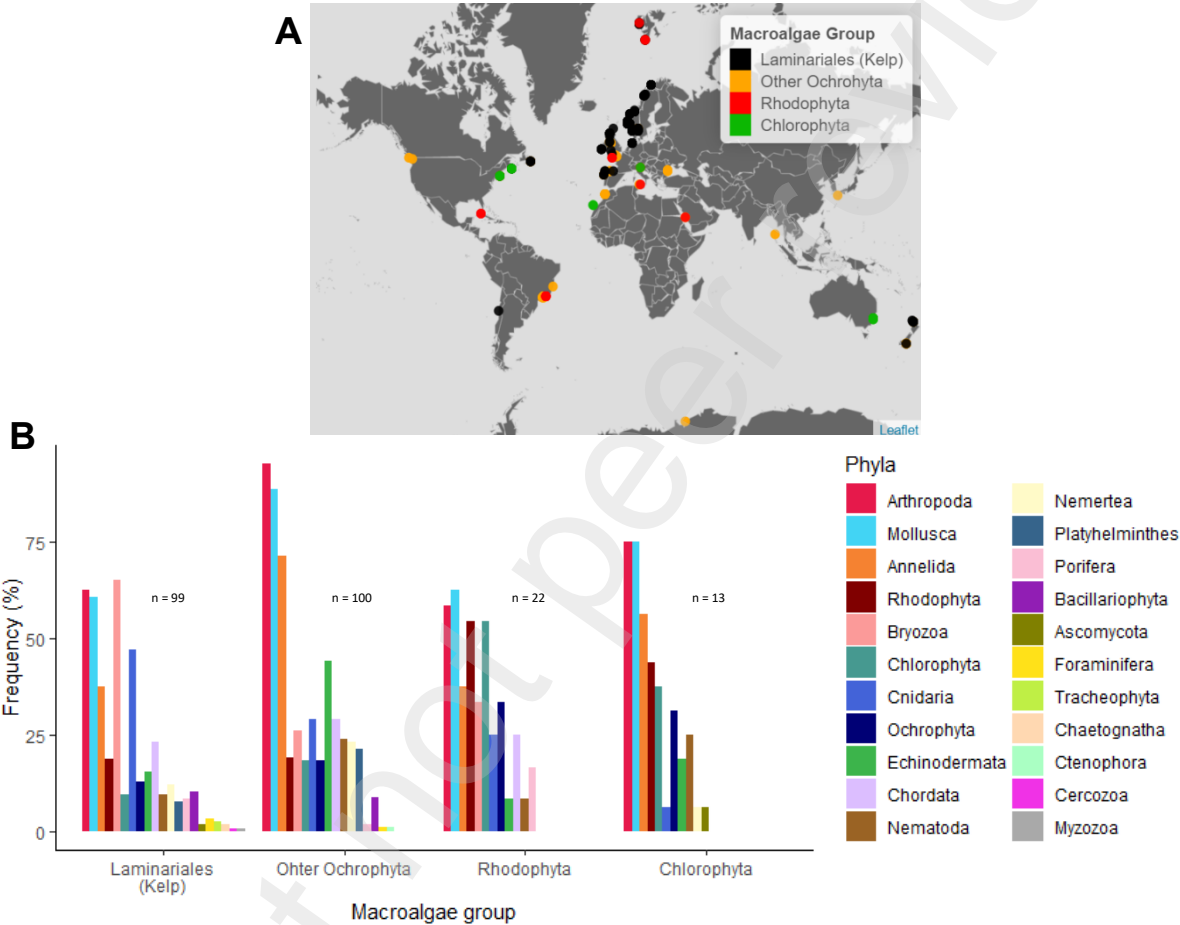


Figure 1. A: Geographical distribution of 55 studies on macroalgae epibiont communities (note that some points overlap). B: Frequency of epibiont phyla observed on each of the four algae group.

The systematic review gathered 5791 observations of epibionts with 62.64 % reported at species level and 92.01 % at least at genus level. In total, 23 different phyla, 45 classes, 122 orders, 675 genera, and 844 species were catalogued. Higher phyla richness of epibionts was observed on Laminariales (phyla richness = 21; mean = 4.17 ± 2.57) and on the other Ochrophyta (phyla richness = 17; mean = 5.19 ± 2.91) than on Rhodophyta (phyla richness = 12; mean = 4.17 ± 2.63) or Chlorophyta (phyla richness = 11; mean = 4.08 ± 2.61).

211 Comparison of epibiont phyla richness and turnover between algal groups

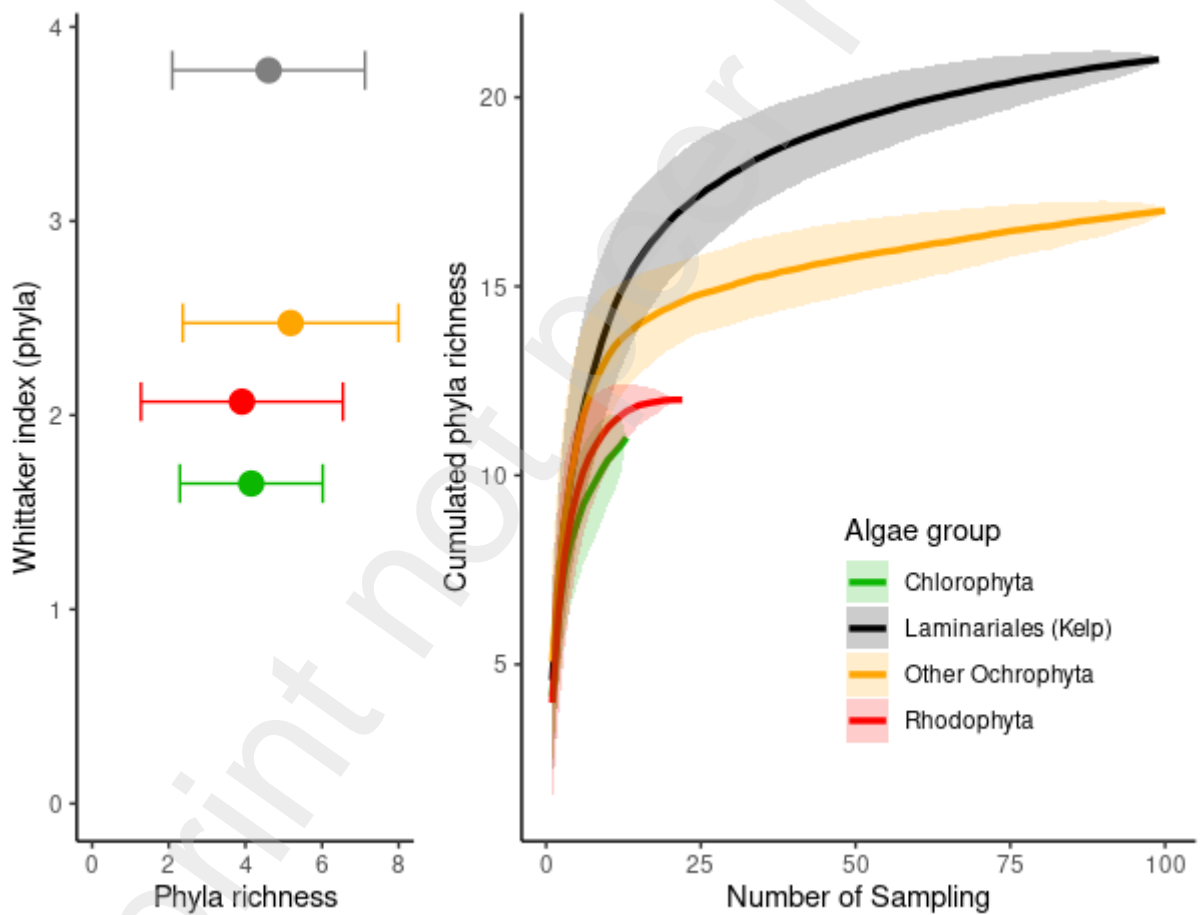
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213 Epibiont phyla richness did not differ between the four algae groups examined (ANOVA, $p = 0.121$) (Figure 2A, x-axis). However, epibiont phyla found on kelp were the most variable between sampling events compared to the other three algal groups ($W_{\text{kelp}} = 3.73$; $W_{\text{Other Ochrophyta}} = 2.47$; $W_{\text{Rhodophyta}} = 2.07$; $W_{\text{Chlorophyta}} = 1.65$) (Figure 2A, y-axis). This was also reflected by the cumulative epibiont phyla by increasing sampling events (Figure 2B). In addition, the levelling-off curves of kelp, other Ochrophyta and Rhodophyta might be indicative that sampling effort within these groups has been more exhaustive than Chlorophyta.

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223 **Figure 2. A: Comparison between the four algae groups of the mean (and 95% error bars) epibiont phyla**
224 **richness (x-axis) and Whittaker's index of epibiont phyla turnover amongst sampling events (y-axis). B:**
225 **Comparison between the four algae groups of the cumulative epibiont phyla richness by increasing sampling**
226 **events. Lines represent mean cumulative phyla richness of a given number of sampling events after 1000**
227 **permutations and shaded areas represent 95% standard error intervals.**

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229 Environmental drivers of kelp epibiont taxa

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231 Irrespective of taxonomic level (Phylum, Class, Order), there was a significantly higher probability of bryozoan
 232 presence on kelp for temperatures below 11°C (Table 2, Figure 3A). Bryozoan presence did not depend on
 233 whether kelp was wild or not wild (i.e. farmed/planted) (Table 2). On the other hand, Cnidaria, and more
 234 particularly hydrozoan presence, was only dependent on whether kelp was wild or not wild (Table 2).
 235 Specifically, a significantly higher probability of hydrozoan biofouling was found on kelp that was not wild
 236 (farmed/planted) compared to wild populations (Figure 4). Finally, the probability of presence of Gastropoda
 237 and Ischyroceridae amphipods significantly increased with salinity (Table 2, Figure 4B).

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239 **Table 2. Effects of environmental variables (chl-a, salinity, SST, wave height and kelp condition (wild vs not**
 240 **wild) on the probability of different epibiont taxa being present or absent on kelp fronds. Results are**
 241 **presented for different taxonomic levels as effects were not always consistent within specific phyla (e.g.,**
 242 **see Gastropoda) and also because for some taxa (e.g. Amphipoda) information might be available only for**
 243 **one family (e.g. Ischyroceridae). Sample size available for the comparison between kelp condition (wild vs**
 244 **not wild) is also provided.**

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Response Variable	Chl-a	Salinity	Temperature	Wave height	Condition	Sample Size			
	LRT p-value	LRT (p-value)	LRT (p-value)	LRT (p-value)	LRT (p-value)	Taxon present		Taxon absent	
						Wild	Not wild	Wild	Not wild
All Bryozoa	0.727 (0.394)	0.236 (0.627)	15.328 (<0.001)	0.001 (1.00)	1.301 (0.254)	30	30	26	13
Gymnolaemata	0.266 (0.606)	0.042 (0.838)	11.202 (<0.001)	0.419 (0.517)	0.499 (0.480)	28	21	28	22
Cheilostomatida (Membranipora)	0.266 (0.606)	0.042 (0.838)	11.202 (<0.001)	0.419 (0.517)	0.499 (0.480)	28	21	28	22
All Cnidaria	2.477 (0.116)	1.501 (0.221)	0.037 (0.847)	0.813 (0.367)	5.839 (0.016)	16	32	40	11
Hydrozoa	1.242 (0.265)	1.160 (0.281)	0.056 (0.813)	0.138 (0.710)	7.800 (0.005)	14	32	42	11
All Gastropoda	0.095 (0.758)	5.968 (0.015)	2.375 (0.123)	0.049 (0.825)	1.133 (0.287)	51	14	5	29

Littorinimorpha	3.017 (0.082)	1.202 (0.273)	0.180 (0.671)	0.469 (0.493)	4.811 (0.028)	29	12	27	31
Ischyroceridae (mostly Jassa)	-0.058 (1.000)	4.682 (0.030)	0.285 (0.593)	0.732 (0.392)	1.143 (0.285)	34	9	22	34

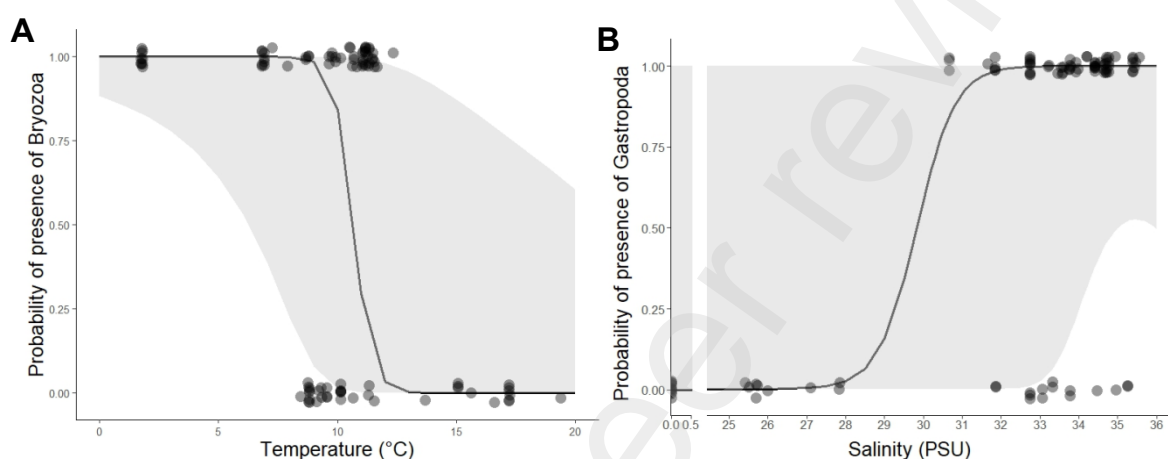


Figure 3. Probability of kelp biofouling by Bryozoa with increasing temperature (A) and gastropods with salinity (B) in the North-East Atlantic. Points represent the presence or absence of the biofouling taxon from the kelp fronts (1-present, 0-absent) using the data collected from our systematic literature review (note that points may overlap). Black lines represent the fitted probability values from the binomial model (see also table 2) and gray funnels represent 95% confidence intervals.

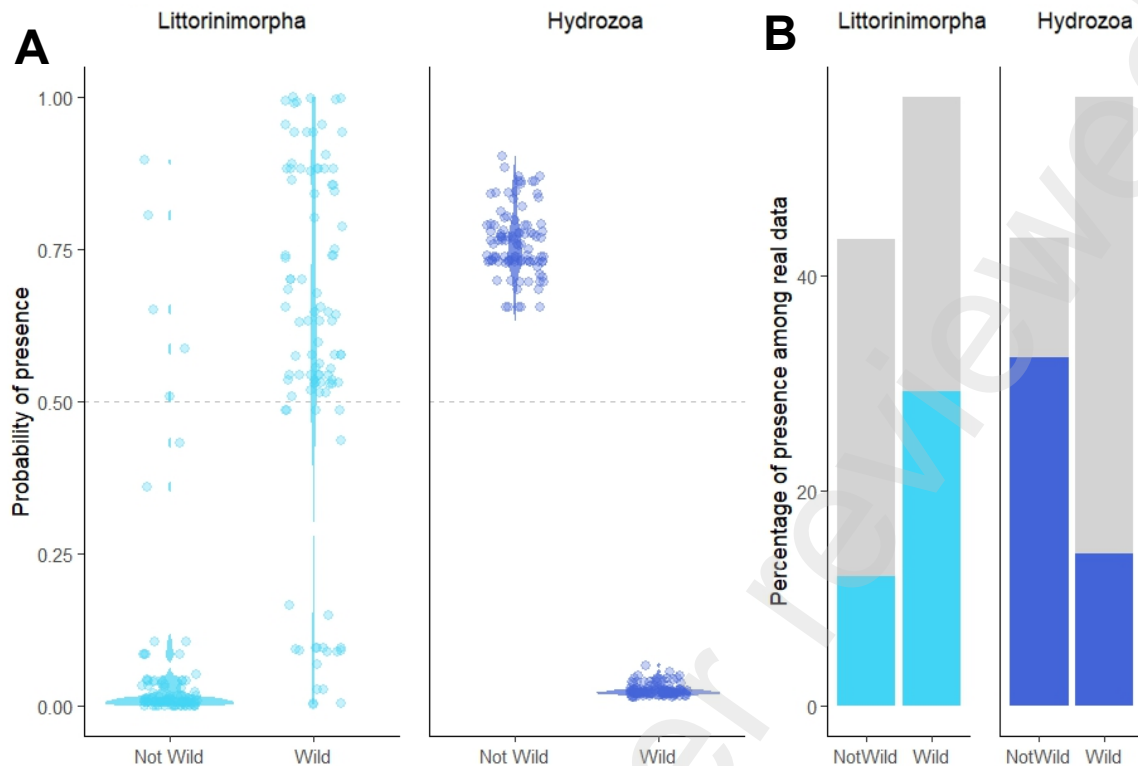


Figure 4. Probability of presence (A) and real data (B) of (A) Littorinimorpha and Hydrozoa according to condition (wild/not wild) of kelp (Laminariales), based on 99 samplings across 26 publications. Note that in panel B the colored part represents presence and gray part represents absence of the taxon.

Using the data from the NASA and Copernicus databases, the mapped probability of bryozoan presence in North-East Atlantic shows a low risk of biofouling at the south of the English Channel, an intermediate area between 53 ° N and 60 ° N where presence is likely to be determined by coastal factors such as cold freshwater inflows lowering the local SST and an area with high risk of biofouling, northern than 58 ° N (Figure 5). We only present the map for bryozoans as this was the only taxon that was consistently affected by temperature across the 3 taxonomic levels and its distribution based on temperature can be clearly visualized according to the large-scale SST patterns. On the other hand, gastropods and amphipods which are more influenced by inshore patterns in salinity cannot be visualized in this map.

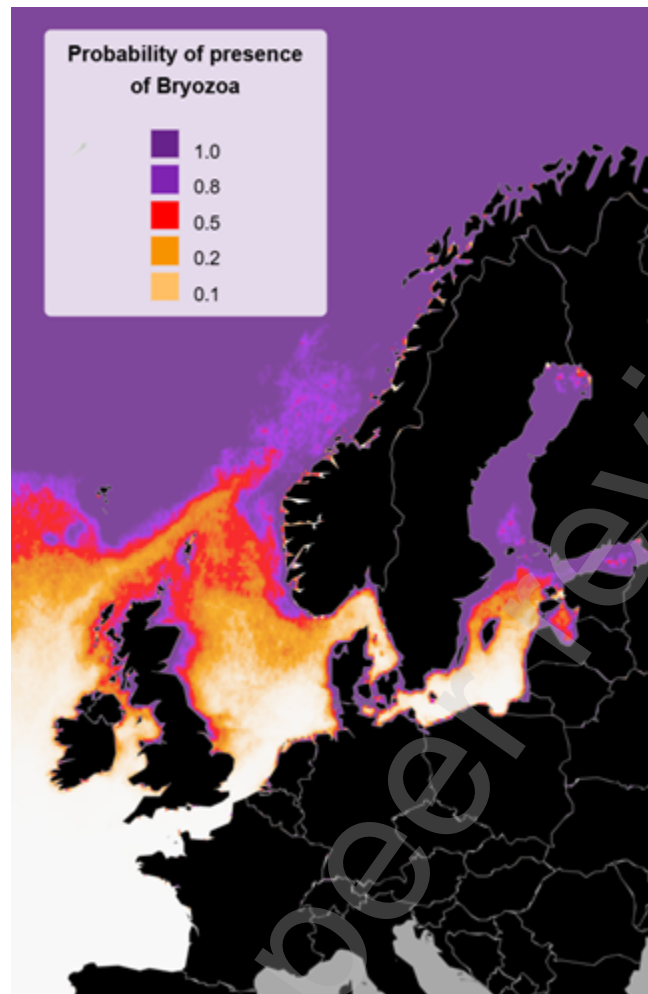


Figure 5. Spatial distribution of kelp biofouling risk by bryozoans for the North-East Atlantic region where currently seaweed aquaculture is rapidly expanding. The spatial prediction was based on our binomial model of bryozoan presence as a function of salinity, SST, kelp condition (wild/not wild), wave height and chl-a, in which the variable SST was found to have a significant effect on the presence. A value of 1 indicates maximum risk of biofouling presence and 0 indicates minim risk.

Discussion

The results of our study provide critical insights into the environmental drivers of macroalgal biofouling, particularly in the North-East Atlantic, where the expansion of seaweed aquaculture is rapidly increasing. Our findings highlight significant variations in epibiont communities, with bryozoans showing a strong dependency on lower SST, while hydrozoans preferentially colonize farmed kelp over wild populations. This differentiation underscores the complex interactions between environmental conditions and biofouling dynamics, suggesting that site-specific factors, such as local salinity and temperature fluctuations, play crucial roles in shaping

epibiont assemblages. By compiling data from multiple sources, we not only identified geographic hotspots of research but also established a foundation for predictive modeling of biofouling risks which can be used to investigate responses to future global warming scenarios. These insights are essential for informing sustainable aquaculture practices and enhancing the resilience of macroalgal farms against the challenges posed by biofouling organisms.

Hydrozoan presence on kelp fronds was not associated with any of the studied environmental covariates. Instead, it was significantly more present on kelp that were not wild (i.e. farmed/planted) than on wild kelp populations. One hypothesis is that the higher density of farmed kelp reduces hydrodynamic forces, creating a more favorable environment for the settlement and growth of hydrozoan larvae (Shi et al., 2011; Walls et al., 2017). It is also possible that hydrozoan benthic predators of hydrozoans (e.g., snails, worms, anemones, crabs) are absent in farmed kelp as they are not in contact with the benthic communities. Another possibility is that as farmed kelp is hanging vertically from the lines, this orientation is favoring more heterotrophic epibionts (Malerba et al., 2019) compared to the fronds of wild kelp which are more exposed to light. Finally, another explanation might be related to density-dependent effects of larvae transmission and settlement between the fronds in the more densely packed cultivated kelp fronds; however, this hypothesis remains to be tested in future studies on the topic.

Bryozoan presence was linked to temperatures below 11°C. The relationship between temperature and bryozoan biofouling remains uncertain in the literature. For example, a model based on 29 sites predicts an increase in bryozoan biofouling with rising temperatures (Pratt et al., 2022), while in situ observations indicate a higher percentage of bryozoan coverage in northern Norway (where water is colder) compared to southern Norway (Førde et al., 2016). Literature specifically addressing bryozoan biofouling on kelp is more prevalent in Norway and diminishes further south, suggesting that bryozoans may be less problematic in more temperate latitudes. Although our analysis incorporated samples from various seasons, bryozoans typically exhibit a strong peak in abundance and coverage around late June, indicating that we may have underestimated their distribution range.

The sensitivity of Gastropoda to low salinity seen in our study aligns with industry mitigation measures where kelp fronds are washed with freshwater to remove gastropods. Our results also align with previous studies, albeit the salinity threshold we identified is more stringent. For example, Rosenberg & Rosenberg (1972) demonstrated that the activity of *Littorina littorea*, a species present in circa 1/3 of our samples, is altered for at least a week following just 12 hours in 15 ‰ salinity. Similarly, *Rissoa parva*, the third most abundant species in our study, has been reported to perish after one week of exposure to salinity levels below 14 ‰ (Warén,

1996). However, many studies have focused primarily on the adult stage, typically at a single temperature, for short durations, and without repeated stress, which may result in an inflated tolerance to low salinity compared to field conditions. In contrast, our threshold represents a yearly mean tolerance, reflecting the overall environmental conditions that a population can sustain.

Since bryozoans and hydrozoans primarily feed by suspension, we aimed to use chlorophyll concentrations as a proxy for food availability. However, kelp is known to grow in highly productive coastal areas where mean chlorophyll concentrations are likely to exceed limiting levels. Measurements of growth rates for *Electra pilosa*, a common bryozoan, indicated a homogeneous range for chlorophyll concentrations between 1.26 µg/L and 6.3 µg/L (Hermansen et al., 2001). In our dataset comprising of 55 macroalgae studies, 85 out of 99 samples collected from kelp sites had chlorophyll concentrations above 1.26 µg/L, with the minimum concentration being 0.856 µg/L. Therefore, it is probable that chlorophyll concentrations in the North-East Atlantic are frequently above limiting levels, thus minimizing the impact of this variable on the growth of most epibionts. However, it should be noted that due to metadata availability limitations, our analysis did not account for seasonal variations, which might have masked the importance of seasonal variations of chlorophyll on epibiont occurrence. This is particularly true given that recent studies have highlighted that fouling intensity is higher in late spring and summer (Corrigan et al., 2023). This limitation in the current dataset, highlights the importance of obtaining original large-scale data on biofouling epibionts over a full annual cycle.

Wave exposure can have pervasive impacts on both macroalgae species composition (Spatharis et al., 2011) and epibiont composition (Visch et al., 2020). Specifically, higher biomass of biofouling and especially hydrozoans have been linked to weak hydrodynamic conditions (Matsson et al., 2019; Visch et al., 2020), whereas specific amphipod epibionts have been linked to high wave exposure (Moore, 1985). However, in our study wave height was not identified as a significant driver of biofouling. The spatial resolution of the wave data was broader than that of other environmental parameters, with a 22 km radius compared to 4-8 km for the others. This reduced spatial discretization between sampling sites likely diminished the statistical power in our analysis. This is particularly the case because wave height and hydrodynamics are highly sensitive to local features such as topography (smooth beach, bay, cliff) and depth.

In conclusion, our results indicate that certain biofouling species are linked to environmental parameters, such as temperature (for bryozoans), salinity (for gastropods), and the type of kelp population (wild vs. not wild) for hydrozoans. Laminariales support richer and more diverse epibiont communities compared to other algal groups, emphasizing the need for further research on the relationship between environmental conditions, community composition, and their effects on macroalgal development. Beyond Laminariales, the diversity in

shape, size, and composition of other algae necessitates a focused approach to develop similar models. Given the challenges of food security and the need to protect coastal ecosystems, leveraging the relationship between biofouling and environmental parameters presents a promising strategy to reduce farming costs and minimize the use of harmful chemicals. To enhance this approach, more in situ data, particularly regarding hydrodynamics, are essential. Additional parameters, such as photoperiod, light intensity, pH, vessel traffic, slope, and substrate type, as well as larger geographical scales, should also be investigated.

Acknowledgements

Financial support for this study was provided by BBSRC Sustainable Aquaculture fund for project BB/Z515243/1 “Improving the sustainability of UK's emerging seaweed industry” as well as Marine Fund Scotland for project SCOMFF1164 Environmental DNA as a tool for preventing seaweed farm biofouling. E.C. received funding from the European Union Horizon 2020 research and innovation program within the framework of the CMMI/MaRITeC-X project under grant agreement no. 857586.

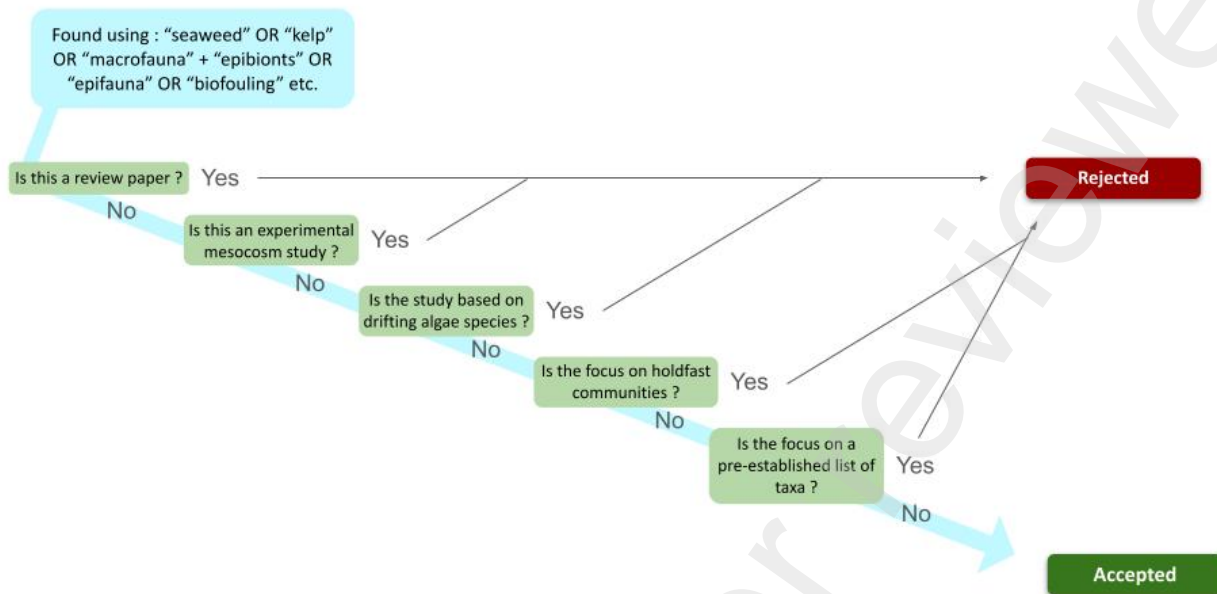
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485 **Figure S1: Selection process of papers on macroalgae epibionts. The research was focused only on**
486 **invertebrate epibionts and not epiphytes.**

488 **Kelpcrofting sampling description. Seaweed species, number of epibionts**

490 Two sites (Scalpay and Pabay) were sampled within ®KelpCrofters Farm (NW Scotland) for epibiont species
491 diversity during a full production cycle and for 2 farmed kelp species (*Saccharina latissima* and *Alaria*
492 *esculenta*). Epibionts were collected across a total of 18 sampling points between December 2021 July 2022.
493 Fronds were collected on site and preserved in absolute ethanol and kept in the freezer (-20°C). Samples were
494 then acclimatized to room temperature and prepared for both morphological under sterile conditions.
495 Samples were first sieved for the specimens not attached, and fronds were carefully rinsed with ethanol.
496 Fronds were then photographed to estimate fouling cover, and epibiont specimens were collected with sterile
497 forceps. All collected specimens new in our records, once morphologically identified under the
498 stereomicroscope (Leica S9i), were photographed and saved for subsequent molecular (barcoding) analyses
499 to assure all species present in our samples were molecularly identified too. Afterwards, specimens collected
500 in each sample were quantified under the stereomicroscope to estimate relative epibionts abundance per
501 frond.