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Local flexibility in feeding behaviour and contrasting microhabitat use of an omnivore across latitudes.

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Authors' contributions: JCL, TW and TdB conceived the ideas and designed the study. TW and TdB obtained the initial funding. JCL, TdB, TW, HC, JF and KFD collected and processed samples during field campaigns. CL processed isotope samples and JCL and FdB analysed the sea urchin guts. JCL analysed the data and led the writing. All authors contributed critically to manuscript drafts and discussion.

ABSTRACT

As the environment is getting warmer and species are redistributed, consumers can be forced to adjust their interactions with available prey, and this could have cascading effects within food webs. To better understand the capacity for foraging flexibility, our study aimed to determine the diet variability of an ectotherm omnivore inhabiting kelp forests, the sea urchin *Echinus esculentus*, along its entire latitudinal distribution in the northeast Atlantic. Using a combination of gut content and stable isotope analyses, we determined the diet and trophic position of sea urchins at sites in Portugal (42°N), France (49°N), southern Norway (63°N), and northern Norway (70°N), and related these results to the local abundance and distribution of putative food items. With mean estimated trophic levels ranging from 2.4 to 4.6, omnivory and diet varied substantially within and between sites but not across latitudes. Diet composition generally reflected prey availability within epiphyte or understorey assemblages, with local affinities demonstrating that the sea urchin adjusts its foraging to match the small-scale distribution of food items. A net “preference” for epiphytic food sources was found in northern Norway, where understorey food was limited compared to other regions. We conclude that diet change may occur in response to food source redistribution at multiple spatial scales (microhabitats, sites, regions). Across these scales, the way that key consumers alter their foraging in response to food availability can have important implication for food web dynamics and ecosystem functions along current and future environmental gradients.

Key-words. Food web, Opportunism, Trophic plasticity, Urchin grazing, *Laminaria hyperborea*, *Echinus esculentus*

INTRODUCTION

Consumptive interactions (i.e., predation) can have major implications for the structure and dynamics of communities (Chase et al. 2009; Vergés et al. 2019) and there are urgent needs for determining their variations under changing climate and biodiversity redistribution (Sentis et al. 2014; Bruno et al. 2015; Rosenblatt and Schmitz 2016). In response to changes in prey abundances, consumers can switch to alternative food items and/or readjust the strength of their interactions with the prey (Sentis et al. 2014; Gilljam et al. 2015). In addition, and especially in the case of ectotherms, some consumptive interactions can be strengthened due to changes in metabolic requirements imposed by changing climate (Bruno et al. 2015; Rosenblatt and Schmitz 2016; Anderson et al. 2017). The magnitude of these changes may, however, vary asymmetrically between predators and prey depending on the differential thermal responses of both resource and consumer traits, such as mobility and strategy to acquire resources (Dell et al. 2014). The diversity of these scenarios is challenging predictions of future food webs and ecosystem functioning (Bruno et al. 2015; Rosenblatt and Schmitz 2016; Kortsch et al. 2019; Vergés et al. 2019).

Latitudinal variation in species interactions has provided critical information on potential future changes with climate warming (Wernberg et al. 2010; Bennett et al. 2015a; Vergés et al. 2019). Large scale comparative experiments from various habitats have strongly improved our general understanding of both the structuring role of consumers on biodiversity gradients (Chase et al. 2009; Freestone et al. 2011; Bennett et al. 2015b; Roslin et al. 2017; Whalen et al. in press) and of the global evolutionary patterns of plant defences and plant-herbivore interactions (Pennings and Silliman 2005; Demko et al. 2017). To our knowledge, however, only a few studies have investigated intra-specific patterns in the activity of consumers across broad climatic gradients. In their latitudinal comparison of the feeding behaviour of the isopod *Idotea balthica*, Bell and Sotka

(2012) revealed that this generalist grazer displayed local preferences for some of the food sources available in different regions. In northeastern America, Anstett et al. (2014) compared the intensity of grazing by different insects on the plant *Oenothera biennnis* and observed every possible relationship (positive, non-significant or negative) with increasing latitude, likely due to plant-herbivore specialization (versus generalism) and herbivore traits. Whether local adaptation or phenotypic plasticity is to be invoked, these two examples support the idea that the trophic position of resident consumers can vary across spatial scales. Notwithstanding its pervasiveness, our current understanding of omnivory (i.e. wherein a consumer feeds on several trophic levels) within taxa across such scales remains highly limited (Clay et al. 2017).

There is a growing interest in understanding how omnivory varies with environmental conditions, especially temperature, which has so far demonstrated mixed results (Rosenblatt and Schmitz 2016; Anderson et al. 2017). The prevailing paradigm that the dietary proportion of carbohydrates increases more than proteins with increasing temperature (because carbon-rich compounds are more readily processed to meet energy demands via respiration), has received experimental support from a range of different ectotherms (marine copepods, caterpillars, freshwater crayfish, tadpoles and insect larvae; Croll and Watts 2004; Lee et al. 2015; Boersma et al. 2016; Carreira et al. 2016). Out of three tadpole species tested by Carreira et al. (2016), however, the most carnivorous species were incapacitated when fed macrophytes in warming conditions. This last result contrasts with the paradigm and suggests that omnivory responses to temperature may instead depend on initial species-specific diets (nutrient limitations), as also supported by stoichiometric models (Anderson et al. 2017) (cf. Sperfeld et al. 2017 for further confrontation of related theorotical frameworks). Increased consumption of protein over carbohydrates with increasing temperature, in order to promote growth, development and survival, has been experimentally shown in a grasshopper fed artificial diets (Schmitz et al. 2016) and more indirectly (through varied C:N) in a beetle fed various plant species (Lemoine et al. 2013). Conversely, in cold conditions, carbohydrate consumption may be enhanced to compensate for reduced energy intake, as also suggested from experiments on the mealworm beetle fed synthetic diets (Rho and Lee 2017). Based on such premises, it is of little surprise to find inconsistent seasonal variations in omnivory across field studies (Miyasaka and Genkai-Kato 2009; Boersma et al. 2016), and calls for additional comparative studies across multiple spatial scales and environments.

In this study, we examined the omnivory of a broadly distributed ectotherm consumer - the sea urchin *Echinus esculentus (*hereafter *Echinus*) - across latitudes that are representative of different climatic conditions. *Echinus* inhabits kelp forests along the latitudinal distribution of the kelp *Laminaria hyperborea,* ranging from Portugal (~ 41°N) to northern Norway (71°N) (Tyler et al. 1995). A substantially varied diet has generally been reported for the species, but has to the best of our knowledge, never been compared across larger spatial scales and environments, in spite of interesting patterns suggested by local-scale studies (see methods). Importantly, animal proteins (and possibly lipids) are seemingly required in *Echinus'* diet to promote its somatic growth and reproductive output (Bonsdorff and Vahl 1982; Kelly et al. 2001). This is also observed in other sea urchins (e.g., Lares and McClintock 1991; Fernandez and Boudouresque 2000). In marine systems, the amounts (per unit of dry mass) of proteins and lipids in sessile fauna are on average 3.2 and 5.5 times higher in than in seaweeds, which contain 3.9 times more carbohydrates than fauna (Brey et al. 2010). Assuming the energy investment in foraging on the two food categories is identical (both being sessile, Dell et al. 2014), we first hypothesized that (1) the sessile fauna intake would be greater in warmer conditions, therefore producing an omnivory gradient across latitudes. While absolute consumption rate could also vary with temperature (Bruno et al. 2015) and thus counterbalance temperature-driven metabolic nutrient limitation (Anderson et al. 2017), we also had the alternative hypothesis that (2) the balance between animal and algal food would vary according to the local availability of food items, hence indicating an entirely opportunistic behaviour uncoupled, at least directly, from climatic conditions. Should omnivory be driven by opportunism, we further hypothesized that (3) the consumer would locally adjust its foraging strategy at multiple spatial scales.

METHODS

Model species

Although the vast array of putative prey of *Echinus* is generally acknowledged and supported by qualitative observations of gut contents made in Western Scotland (Comely and Ansell 1988; Emson and Moore 1998), the Isle of Man (Moore 1934) and the English Channel (Leclerc et al. 2015), information regarding broad spatial variations in diet is generally lacking. Differences in gonad condition across shallow and deep sites reported in previous studies have often been attributed to contrasting diversity and availability of food items (Moore 1934; Nichols et al. 1985). In addition, local-scale studies using stable isotopes have indicated that *Echinus* has a substantially varied diet largely dominated by kelp in Norway (Fredriksen 2003) and by sessile fauna in France (Leclerc et al. 2015). Whether these differences in diet reflect local response to available food sources, changes relating to metabolic requirements or is incidental (e.g., as a function of different temperature regimes) is unresolved.

Study sites and sampling

The sampling design consisted of four regions (separated by 1000s of kilometres), with two sites (separated by 1-10s km) nested within each region. The study area ranged from northern Portugal (41.6°N) to northern Norway (69.6°N), hence covering 28° of latitude (Table S1). Mean sea surface temperatures (extracted from the Bio-Oracle database; Tyberghein et al. 2012; Assis et al. 2018 for the period 2000-2014, Table S2) ranged from 7.0°C in northern Norway (average minimum and maximum between 3.3 and 11.3°C) to 15.6°C in Portugal (between 13.0 and 18.2°C). Over the same period, long-term temperature variations were weak in Portugal (range of ~ 5°C) and France (6°C), under the direct influence of the Gulf Stream, moderate in northern Norway (8°C) and comparatively greater in southern Norway (10°C). Each study site was haphazardly selected among *Laminaria hyperborea* forests at a depth of 5-12 m below chart datum. Adult *Echinus* were 'frequent' (SACFOR scale) at all study sites (1-9 ind. 10 m^{-2}). Within each study site, 16 to 20 sea urchins, 6 young (stipe < ca. 5cm) and adult (stipe > ca. 5 cm) kelps were haphazardly collected by divers, kept on ice and then processed in the laboratory within 12 hours. Within the framework of distinct field campaigns, sampling was done in spring 2014 in France and southern Norway, in spring 2015 in Portugal and in summer 2016 in northern Norway.

The abundance of primary producers and all potential urchin food sources (including sessile fauna) were assessed using two distinct methods. At the site scale, the fleshy seaweed biomass (wet weight: blotted with paper tissue and weighed) was determined at the lowest taxonomic level possible (generally species) from destructively sampled 0.25 m^2 quadrats. In the laboratory, seaweed biomass was further subdivided into two categories, either epilithic (on bedrock) or epiphytic (on kelp stipe). In addition, a series of independent photos were taken to determine the abundance of all potential food sources (including fauna) within the main strata of the kelp forest: bedrock (n = 5-11) and stipe (n = 5-11). These potential food sources were classified using morpho-functional groups of seaweeds and sessile fauna, which have proven relevant to address ecological functions of complex stratified systems such as *Laminaria hyperborea* forests (see Appendix S1). Percentage covers of morpho-functional groups of seaweeds and sessile fauna were visually estimated by the same observer (JCL) from photos for each potential food source. These estimations followed the Dethier et al. (1993) framework, by summing semi-abundance either over sub-quadrats of the quadrats (0-4 × 25) or over linear (vertical) portions of the stipe (0-10 × 10). Most fleshy seaweeds and their epiphytes (notably sessile fauna) were generally visible in photos, making easier their abundance estimation easier. In both habitats, however, most understorey taxa (crusts and small sessile fauna) or habitat features (sediment) could not be quantified and were thus likely underestimated. While percentage cover were assessed with a fixed scale of 0.1 m^2 on the bedrock, stipe area available to colonization by epiphytes varied across kelp individuals and was not quantified. Nonetheless, differences in surface area (among stipes or between stipes and quadrats) were not considered an issue in the context of our study since relative values of cover, based on similar sampling intensity and broad functional groups (rather than species) were only compared among these strata and gut contents (see section on data analyses).

Urchin diet and trophic position

In the laboratory, sea urchins were processed for a series of morphological parameters, such as their size (maximum test width) and gonad index (ratio between gonad and total wet biomass). Aristotle’s lanterns and guts were dissected and stored in separate Ziploc bags at - 30°C until further analysis. Unlike stable isotopes which give a time-integrative estimation of diet, gut contents give a snapshot of feeding choices but are more robust to determine preferences and opportunism. Gut contents also provide accurate information about prey species which have been ingested and are therefore useful in determining individual habitat use and foraging strategies, within and among sites (Vanderklift et al. 2006).

Gut contents from individual sea urchins were analysed in order to determine any food preferences. To facilitate identification, gut contents were washed thoroughly with freshwater through an 80 µm mesh sieve. Each gut sample was then placed within a Dollfus's dish (50 × 100 × 8 mm), where the bottom was divided into 200 square compartments (5 × 5 × 2 mm). Although crushed by the sea urchin teeth over ingestion and reduced to < 2-5 mm pieces within faecal pellets, most prey items are readily identifiable using a series of morphological and histological traits (e.g. Emson and Moore 1998). For each food item category (morpho-functional group, Appendix S1), a score was given according to its occurrence over the total number of occupied squares. Each food item score was finally reported as a percentage, the sum of which frequently exceeded 100% given the over-layering of food item categories within the bulk sample.

Stable isotope analyses were conducted on individual urchins and on the biomass-dominant primary food source in order to estimate urchin trophic level. *Laminaria hyperborea* was expected to be the most abundant fleshy seaweed (except in Portugal, see results) and the only seaweed shared across all study sites. Within kelp forests, *L. hyperborea* also represents the dominant trophic resource of sessile suspension-feeders (e.g. barnacles, bivalves, bryozoans), which can be a major component of *Echinus* diet (Leclerc et al. 2013; 2015). Given these reasons and in the absence of suspension-feeders isotope values (see also Post 2002) collected for this study, *L. hyperborea* was chosen as baseline, using average δ^{15}N values of adult and young kelp individuals, generally in the range of other seaweeds (Leclerc et al. 2013). Clean sections of kelp (ca. 4 × 4 cm) were dissected from newly-formed lamina on freshly collected adult kelp and around the meristem (stipe and lamina) on young kelp. For *Echinus*, muscle tissues, reflecting time-integrative assimilation of sources (e.g. Pinnegar and Polunin 1999), were dissected from the Aristotle's lantern. Each sample was checked and when necessary cleaned from epiphytes using a scalpel, thoroughly rinsed with filtered seawater, then oven-dried at 55°C for 48 h. Because δ^{15}N values were targeted, no further treatment was deemed necessary. Dried samples were ground using an agate mortar and a pestle, then put in tin capsules for mass-spectrometry analyses.

Nitrogen isotope-ratios were determined using a Flash EA-CN analyser coupled with a Finnigan Delta Plus mass spectrometer, via a Finnigan Con-Flo III interface. Data are expressed in the standard δ unit, calculated in relation to the certified reference material atmospheric dinitrogen (at-air): $\delta^{15}N = [(^{15}N/^{14}N_{sample} / ^{15}N/^{14}N_{reference}) - 1] \times 10^3$. The at-air scale was calibrated against IAEA-N2 and USGS34 international standards, using a two-point normalisation (Paul et al. 2007). In addition, a laboratory standard (casein IRMS certified standard, B2155 Elemental Microanalysis Ltd, UK) is used throughout the analyses, as quality check. The standard deviation of repeated measurements of δ^{15}N values of a laboratory standard was 0.05 ‰ versus at-air.

Data analyses

Estimation of trophic level using stable isotopes

Isotopic analyses helped to estimate trophic levels of each individual urchin (TL_{urchin}): $TL_{urchin} = 1 + (\delta^{15}N_{urchin} - \delta^{15}N_{baseline}) / DDDF$, where $\delta^{15}N_{baseline}$ corresponds to the mean δ^{15}N of kelp (averaged over adult and young kelps per site) and DDDF corresponds to diet-dependent discrimination factor ($\Delta^{15}N$) calculated for each site according to Caut et al. (2009). This method was chosen due to the omnivory of *Echinus* and given the large variability in kelp $\delta^{15}N$ observed among sites (see also Figure S4). No discrimination factor has been proposed for sea urchins (e.g.,Vanderklift et al. 2006) and the use of a fixed $\delta^{15}N$ led to contradictory results in comparison with gut contents analyses (overestimation of TL at sites where kelp were poorly enriched in ^{15}N). In addition, dependency between diet $\delta^{15}N$ and discrimination factor has been experimentally demonstrated in other echinoderms (Blanchet-Aurigny et al. 2012).

Statistical analyses

All univariate and multivariate data were analysed using the same two-way nested PERMANOVAs, with 4999 permutations and the random factors ‘region’ and ‘site’. Univariate and multivariate analyses were respectively based on Euclidean distance and Bray-Curtis similarity matrices. Univariate data included urchin size, gonad index and trophic level as well as the abundances of the dominant groups of putative food items (biomass of kelp and other seaweeds, percentage cover of seaweeds and sessile fauna), on either bedrock or stipe. Multivariate data consisted of the relative abundances of each food item categories within gut contents. Prior to analyses, the homogeneity in univariate or multivariate dispersion was checked among the levels of the factor ‘region’ using PERMDISP (Anderson et al. 2008). When assumption of homoscedasticity was not met after any transformation of univariate data, the analysis was conducted on untransformed data following Underwood (1997) and a more conservative level of significance ($\alpha = 0.01$) was taken into account. For multivariate structure, samples were also ordinated using non-metric multidimensional scaling (nMDS) to support PERMANOVA results (Anderson et al. 2008). In order to strengthen all these analyses, we also examined how the variation was distributed across all three nested levels tested (region site, residual). When a negative component of variations was found, it was set to zero and the model was adjusted in order to re-calculate the remaining estimates (Fletcher and Underwood 2002).

Foraging strategies were determined from gut content similarities with prey distribution in the sea urchin environment. At the site scale, the natural habitat-complexity of *L. hyperborea* forests challenges the collection of abundance data for all possible food sources (Christie et al. 2003; Leclerc et al. 2016). More information can, however, be obtained from the abundances of resource on two kelp forest strata known to be visited by *Echinus*: the understorey (on the bedrock) and the epiphytes (on the stipe). We thus developed a relative and binary feeding behaviour index for each of these two strata. First, abundance (cover) data of the main food item categories (except kelp) in different habitats (bedrock and stipe) and within urchin guts were all compiled in a unique matrix. We did not include kelp in the analyses because they were often observed in the urchin diet as a varying mixture of fragment types (ranging from a relative scale of soft to hard tissues, with or without cortex, etc.), which could hardly be assigned to understorey or stipe. Indeed, these diverse type of tissues can be found in varying abundances within either canopy kelp individuals (Kain 1963), understorey young individuals, or detritus (Filbee-Dexter et al. 2018). Second, a matrix of dissimilarity between all pairs of samples was created using the Bray-Curtis index calculated from untransformed data. Third, for each site, principal coordinates were calculated from the Bray-Curtis dissimilarity (non-metric) matrices in order to extract Euclidean distances (metric) between all pairs of samples, while preserving the properties of the Bray-Curtis index. Fourth, for each individual urchin, the average distance between its diet and the food item abundances in each of its putatively targeted habitats (stipe or bedrock) was then calculated. Fifth, the relative and binary feeding behaviour index (FBI) was subsequently calculated for each individual, based upon Armas et al. (2004), as follow: FBI = ($D_{d\text{-}h1}$ – $D_{d\text{-}h2}$)/ ($D_{d\text{-}h1}$ + $D_{d\text{-}h2}$), where $D_{d\text{-}h1}$ = multivariate distance between individual diet and the habitat 1 (here bedrock) and $D_{d\text{-}h2}$ = distance between individual diet and the habitat 2 (stipe). This FBI presents a continuous scale and ranges between – 1 and + 1 indicating a marked (and theoretical) affinity for habitats 1 and 2, respectively. Finally, in order to determine whether urchins present a significant "preference" for one habitat or another at the local scale, PI values were compared to 0 using one-sample *t*-tests within each site. The latter analysis was performed using SigmaPlot, while PERMANOVAs, nMDS and PERMDISPs were performed using PRIMER 7 with PERMANOVA add-on (Anderson et al. 2008).

RESULTS

Across sites and regions, a total of 131 sea urchins were analysed and presented consistent regional differences in both size (test diameter) and wet weight (ww) between core (France, southern Norway) and edge (Portugal, northern Norway) regions (Table 1, Fig. S1). Sea urchins were significantly smaller in Portugal (85.3 ± 7.4 mm, mean ± SD) and northern Norway (78.1 ± 12.3 mm) than in France (113.3 ± 10.1 mm) and southern Norway (110.8 ± 15.7 mm). Likewise, and in spite of within-region significant effects, sea urchins were three times lighter (85.3 ± 7.4 g_{ww}) in Portugal (274.4 ± 62.5 g_{ww}) and northern Norway (224.6 ± 107.6 g_{ww}) than in France (778.3 ± 222.8 g_{ww}) and southern Norway (673.5 ± 217.3 g). Their gonad index varied substantially within sites (72% of variation due to residuals in the model, Table 1) but did not vary among regions (on average 7.2 ± 4.04, Fig. S1). Interestingly though, this index displayed significant site-to-site differences in both Portugal and northern Norway (Table 1, Fig. S1).

Contrasting patterns in food availability at multiple spatial scales

Food availability varied markedly across different spatial scales (among regions, sites, micro-habitats), and depended on food type. *Laminaria hyperborea* dominated the seaweed biomass from France (5.6 ± 4.5 kg_{ww} m^{-2}, mean ± SD) to northern Norway (13.7 ± 11.3 kg_{ww} m^{-2}, Fig. 1A, Table 1), where similar values were observed, but its biomass was much lower (< 0.1 kg_{ww} m^{-2}) in Portugal, where the canopy was dominated by the pseudo-annual kelp *Sacchoriza polyschides* (0.9 ± 0.3 kg_{ww} m^{-2}, Fig. 1B). The epiphyte biomass was statistically similar among regions (Fig. 1C, Table 1), and highly variable within and among sites (cf. *%var*. in Table 1). It is noteworthy that epiphyte biomass was virtually zero at all sites in Portugal and at the Hekkingen site (cf. Table S1) in northern Norway. Significant regional differences were detected for the understorey biomass (Fig. 1D). In northern Norway, the fleshy algal understorey was patchy, monospecific (*Desmarestia aculeata* and the biomass was negligible (5.1 ± 15.6 g_{ww} m^{-2}) when compared to other regions (Table 1, Fig. 1D). Understorey biomass was similar in France (80.4 ± 78.1 g_{ww} m^{-2}) and southern Norway (84.6 ± 831 g_{ww} m^{-2}) and about ten-fold lower than in Portugal (775.9 ± 665.5 g_{ww} m^{-2}, Table 1, Fig. 1D). Similar spatial patterns were shown when fleshy seaweeds were quantified using percentage cover with only the epilithic algae differing significantly between northern Norway (10.0 ± 7.1%, dominated by crusts, Fig. 2) and the other regions (on average 55.9 ± 16.1%, Table 1, Fig. 2). In contrast, neither the percent cover of sessile fauna associated with the stipes or with the bedrock differed among regions, but both displayed substantial site-to-site variations in France and northern Norway (Table 1, Fig. 2).

Diet and omnivory vary substantially in space, but not with latitude

Both stable isotope and gut content analyses were indicative of omnivory, without preference for a specific food source (Fig. 3, Fig. S4). A total of 22 food items could be identified in the sea urchin guts, including diverse morpho-functional groups of seaweeds (including kelp across all study sites), sessile and mobile fauna (Fig. S3). Within faunal groups, barnacles (Cirripeda) and bryozoans displayed the greatest contribution to the urchin diet (Fig. 3B). In spite of a great site within region effect, the multivariate structure of the diet varied significantly among regions (cf. PERMANOVA). However, pairwise tests only reveal statistical difference between Portugal, southern Norway and northern Norway; all diets were similar to samples from France (Table 1, Fig. 3C). The trophic level varied substantially between sites within region in Portugal, France and northern Norway, and no difference was detected among regions (Table 1, Fig. 3A). For instance, the trophic level in France

Adjustment of foraging strategy at multiple spatial scales

Analysing the similarity between the generalist diet and the distribution of its putative food items proved efficient to infer spatial patterns in foraging strategies in space, here between two kelp forest strata: the bedrock and the stipe (Fig. 4). Although broad groups of sessile taxa were considered, the community (or functional) structure of these strata differed significantly within and across study sites (Table S3, Fig. S2). Based on these cover data, sea urchins displayed significant net affinity for one habitat or another in 6 out of the total 8 sites (Fig. 4). Within regions, consistent affinities for the understorey habitats were observed in Portugal whereas consistent affinities for the epiphyte habitats were found in northern Norway. Site-specific affinities for the understorey were also observed in France and southern Norway (cf. also site within region effect, Table 1), but it is noteworthy that many individuals (15.5%) from southern Norway displayed a net affinity for the epiphytes (PI ranging from + 0.05 to + 0.18, Fig. 4A).

DISCUSSION

Consumers are expected to adjust their diet and/or the strength of their interactions in response to the redistribution of their food items and to metabolic changes imposed by global warming (Bruno et al. 2015; Gilljam et al. 2015; Rosenblatt and Schmitz 2016; Anderson et al. 2017). Our results show that neither diet nor trophic level of an omnivore sea urchin inhabiting kelp forests varied significantly among regions across approximately 28° latitude on the NE Atlantic, suggesting that temperature or other covariates of latitude did not influence, at least directly, the feeding preferences of this ectotherm. With respect to variations among sites, however, the diet of sea urchins varied according to local availability of food items. By using a feeding behaviour index, our results further indicate that sea urchins locally adjusted their foraging strategy among kelp forest strata, consistent with great functional plasticity.

Consistent omnivory across latitudes

Metabolic scaling theory (Bruno et al. 2015), the foraging strategy towards sessile prey (Dell et al. 2014) and previous published diets of *Echinus* from local studies (Fredriksen 2003; Leclerc et al. 2015) suggest that animal (protein rich) food intake of this sea urchin should decrease with ocean warming, and therefore with increasing latitude. Although we do not provide evidence on possible individual diet adjustments with temperature (within populations), the latitudinal hypothesis (among populations) is generally rejected by this study. By analysing both gut contents and stable isotopes, our results indicate that *Echinus* maintains omnivory (algal versus animal contribution to the diet) across its latitudinal range. Should temperatures experienced by the sea urchin across its latitudinal range have any influence on its metabolic requirements, our results would align best with models in which stoichiometric imbalance, and dietary preferences, can be preserved by overall increased intake with temperature (Anderson et al. 2017). While temperature is most likely to affect per capita interaction strength, it does not seem to affect *Echinus* food preference at the latitudinal scale studied. Diverse groups of algae and animals were consistently identified as part of the urchin diet at all study sites (e.g. bryozoans, barnacles, kelp and fleshy seaweeds) and nothing indicated a latitudinal shift in their respective abundance. Using stable isotopes ($\delta^{15}N$), estimates of trophic level generally aligned with the relative abundance of food items in digestive contents and previous local studies. For instance, the highest trophic level (4.6 ± 0.2) observed in Roscoff (France) is consistent with Leclerc et al. (2015) estimations in a nearby locality (TL = 4.0), wherein a similar diet was observed. The lowest trophic level (2.4 ± 0.2) estimated in Hekkingen (northern Norway) was also consistent with a kelp-dominated diet shown by gut content analyses. While the trophic level was consistent across regions, it varied markedly among sites within region, providing support to alternative hypotheses, notably related with food availability (see following sections).

Omnivory reflects local food availability across multiple spatial scales

The overall site-to-site variability in both $\delta^{15}N$ and gut contents suggests that spatial patterns in omnivory may be driven mainly by opportunism (in response to food availability) as opposed to latitudinal characteristics of the environment. While feeding trials would have provided empirical evidence for this hypothesis (Bell and Sotka 2012; Demko et al. 2017), qualitative site-to-site comparisons of the heat-maps illustrating the abundances of putative food sources within the understorey (Fig. S2) and the contributions of each food item to the diet of *Echinus* (Fig. 2-3, Fig. S3) shed some light on this pattern. For instance, filamentous algae were virtually absent from gut contents in all sites, except in southern Norway where they dominated the understorey and represented a major component of the urchin diet, regardless of likely limited benefits for macro-consumers (Steneck and Watling 1982). As previously suggested in local studies (Emson and Moore 1998), our results support that site-to-site differences in diets are mostly driven by food availability. These differences could also be reflected in *Echinus* phenology (Moore 1934; Nichols et al. 1985; Comely and Ansell 1988) but we note in that context that relationships between the spawning cycle and diet are generally unresolved for *Echinus*, unlike other well-studied sea urchins (Minor and Scheibling 1997; Fernandez and Boudouresque 2000). Spatial variations in gonad index and food availability can either be consistent (e.g. between young individuals living in faunal-dominated deep reefs and adults living in seaweed rich-shallow reefs, Moore 1934; Nichols et al. 1985) or counter-intuitive (e.g. with considerable variations in the timing of spawning events between apparently similar sites, Comely and Ansell 1988). Likewise, much site-to-site variations in gonad index were observed in both Portugal and northern Norway. While this variation coincides with site-to-site differences in sea urchin size in Portugal (see also Moore 1934), it rather coincides with substantial site-to-site differences in diet and availability of attached fleshy seaweeds (seasonally consistent, KFD, pers. obs.) in northern Norway. These complex relationships certainly deserves attention beyond the scope of this study.

The extent to which the urchin diet and omnivory depend on food availability is further indicated by our feeding behaviour index, which may help to inform of the underlying processes and ecological implications of such flexibility at multiple spatial scales. The consistent occurrence of certain food items in diets at all sites suggests that some of them could be important to the urchin fitness (e.g. kelp, fleshy seaweeds colonized by crustose bryozoans, Bonsdorff and Vahl 1982). In order to obtain these food items in heterogeneous habitats, the sea urchins may be forced to adjust their foraging strategies at the local scale (cf. *Paracentrotus lividus* in seagrass meadows, Camps-Castellà et al. 2020). Because the abundance and distribution of food items across kelp forest strata can vary consistently across broad diversity gradients (e.g. some broadly distributed taxa are exclusive to kelp stipes, Kain-Jones 1971), local adjustments in foraging strategies are likely to create gradients in *Echinus* function at a larger scale.

At the southern (warm) edge of *Laminaria hyperborea* distribution (Portugal), kelp were reduced to small individuals with little to no epiphytes, and there was virtually no stratification (i.e., canopy/sub-canopy) of the kelp forests. In the same region, our index revealed a net affinity for the understorey, where the seaweed biomass was concentrated (Fig. 3B, Fig. S3) and included the few species observed on the stipe (e.g. *Rhodymenia* sp.). Range centre populations of *Echinus* in France and southern Norway were in different kelp forest conditions compared to Portugal, and had access to both epiphytes and understorey seaweeds. *Laminaria hyperborea* forests were similar within and between these two regions, with the prevalence of large kelp individuals (main biomass) loaded by abundant epiphytes (including kelp). The same sites in France and southern Norway were also accompanied by diverse seaweeds and sessile animals growing on the surrounding bedrock. In these kelp forests, our feeding behaviour index suggests that *Echinus* can encounter most of the needed food items in the understorey habitat, although net affinities for either habitat were not significant at two of these sites (Fig. 4). These patterns contrast with northern Norway, where a net affinity for epiphytes was observed. Although abundant epiphytes were found at one site, the understorey habitat at both these sites was generally depauperate and mainly covered by crustose seaweeds, when compared to other regions. If food becomes limited in the understorey, climbing up kelp stipes is probably the best way for a sea urchin to diversify its diet (Bekkby et al. 2015). Consumers venturing on the upper part of stipe can actually access *Palmaria palmata*, which is probably the most palatable red seaweed in the subtidal NE Atlantic kelp forests (Guiry and Blunden 1991; Schaal et al. 2010). Commonly encrusted by the bryozoan *Electra pilosa*, *P. palmata* was herein observed in varying abundance as (and only as) epiphytes from France to northern Norway, and this combination of food items made up the entire diet of some individuals from several of the studied localities (JCL, pers. obs.). Further work would be needed to determine the prevalence of possible individual preferences within the sea urchin populations. More interestingly, it is worth noting that *Echinus* is coexisting with *Strongylocentrotus droebachiensis* (at densities of ca. 0.5 to 1.2 m^{-2}, Filbee-Dexter et al. 2020) in northern Norway. Should that voracious sea urchin be involved in the control of understorey algae (cf. Christie et al. 2019 and references therein), our feeding behaviour index would thus mirror that competition for food resource affect the foraging flexibility of *Echinus*, and force it to browse another habitat (Fig. 4B). This point deserves further attention.

Potential implications of the scale-dependent foraging strategies of Echinus esculentus for kelp forest functioning along NE Atlantic.

While the importance of habitat-forming species, such as kelp, for biodiversity is generally acknowledged, it is noteworthy that not all kelp species share the same habitat-forming traits (e.g. Wernberg et al. 2019 and references therein). Compared to other kelp, the stipe of *L. hyperborea* possess a series of traits conducive to colonization by abundant perennial and semi-annual epiphytes (reviewed in Teagle and Smale 2018), within which diverse and abundant assemblages of fauna can develop and fuel local and adjacent food webs (Norderhaug et al. 2005; Leclerc et al. 2013). Across diverse taxa or morpho-functional groups, sessile epiphytes are indeed characterized by varied structural complexity which have been shown to influence macrofaunal diversity and community structure, at multiple spatial scales (Norderhaug 2004; Norderhaug et al. 2014). A single stipe of kelp can be inhabited by up to 85 macrofaunal species (Leclerc et al. 2016), with abundances that can exceed 80,000 individuals (Christie et al. 2003) and may constitute a microscale diversity refuge in disturbed areas (Leclerc et al. 2015). Although the present data do not provide quantitative evidence for urchin-epiphyte interactions, they align with Bekkby et al. (2015) who demonstrated that *Echinus* can significantly reduce the abundance of kelp epiphytes in mid-Norway, and thus alter the function of this microhabitat. Interestingly, those authors observed a stronger control of epiphytes in 'young' kelp forests undergoing a process of recolonization post-overgrazing by *Strongylocentrotus droebachiensis*, compared to *Echinus*, which were likely more limited by food availability. The paucity of understorey seaweeds in northern Norway as compared to other regions, regardless of the underlying processes (light limitation, grazing by *S. droebachiensis*), is thus likely to exacerbate *Echinus* effects upon the diversity and community structure at local scale in these kelp forests.

Kelp was a minor component of the sea urchin diet at all but one site. Kelp contributed to 30.6% at the northernmost site (Hekkingen, northern Norway), where alternative food items were poorly represented. The most probable explanation for this pattern is that *Echinus* switches to a kelp-dominated diet only when other food items are limited (even epiphytes were virtually absent locally). This has been seen in previous studies conducted in both UK and Norway: negative effects of *Echinus* on kelp – and more specifically recruits – are generally observed in “transition” areas, including the lower vertical (i.e. depth) distribution limit of kelp (Jones and Kain 1967), overgrazed areas (Hagen 1983), and localities or patches undergoing a recovery post-harvesting (Steen et al. 2016). On the other hand, our results revealed that kelp presented similar contributions to the urchin diet in Portugal as compared to other regions, although their biomass in the urchin habitat was ten-fold lower. Even as a minor component, kelp are rich in carbohydrates and may actually be essential to the mixed diet of the sea urchin. Whether the stronger effect of *Echinus* on kelp observed in transition areas and lower depth limit can hold for the southern edge of *L. hyperborea* distribution may be worthy of further investigation (Fig. 4).

In conclusion, we show that the diet and trophic level of an omnivore inhabiting kelp forests, are consistent across four NE Atlantic regions spanning approximately 28°latitude, despite large differences in habitat structure, temperature, and prey availability. Our results however suggest that generalist consumers can adjust their diet and foraging strategies in response to resource availability at multiple scales. While such plasticity may confer to widely distributed generalist consumers (incl. omnivores) a certain resistance to changing environments and habitats, context dependent feeding behaviour challenges our understanding of associated food webs in response to multiple stressors and biodiversity redistribution.

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Table & figure captions

Table 1. Results of PERMANOVA tests for differences in general response variables among levels of the nested factors (region and site). Degrees of freedom (*df*) and components of variation (*var*, expressed as percentages) are indicated for each factor and response variable. Transformations (Transf) and PERMDISP tests (Disp, for the factor region) are summarized. ^{ns}: non-significant, ^{m}: marginally significant at $\alpha = 0.07$, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$. Based upon more or less conservative levels (see "Methods" section), significant values are in bold.

Response variable	Transf	Disp	PERMANOVA Factor			
			F Region (Re)	*F* Site (Si)	*df* Re, Si, Res	*%var* Re, Si, Res
Seaweed biomass (kg m-2)						
Laminaria hyperborea	FORT	ns	**74.70****	0.60ns	3, 4, 38	79, 00, 21
Other kelp	none	*	**16.61****	**8.50*****	3, 4, 38	83, 09, 08
Epiphytes	none	***	1.68ns	2.56*	3, 4, 38	11, 19, 70
Understorey	LOG	ns	**60.75****	0.76ns	3, 4, 38	80, 00, 20
Seaweed cover (%)						
Epiphytes	ASIN	ns	3.75ns	1.33ns	3, 4, 62	17, 03, 80
Understorey	none	*	**32.25****	1.41ns	3, 4, 62	75, 01, 24
Sessile fauna cover (%)						
Epiphytes	ASIN	m	1.31ns	**8.28*****	3, 4, 62	07, 42, 51
Understorey	none	ns	0.46ns	**4.69****	3, 4, 62	00, 34, 76
C:N						
Laminaria hyperborea adults	SQRT	ns	**21.75***	**3.32***	3, 4, 40	80, 05, 15
Laminaria hyperborea young	LOG	m	**22.39****	2.26ns	3, 4, 40	77, 04, 19
E. esculentus	none	***	90.38*	0.48ns	3, 4, 122	78, 00, 22
d15N						
Laminaria hyperborea adults	none	ns	**56.36*****	0.79ns	3, 4, 40	78, 00, 22
Laminaria hyperborea young	none	***	1.68ns	**18.26*****	3, 4, 40	21, 59, 20
E. esculentus	none	***	1.71ns	**147.75*****	3, 4, 122	24, 68, 08
Urchin morphometry						
Diameter (width)	none	m	**37.53****	2.10ns	3, 4 ,123	69, 02, 29
Wet weight	none	***	**20.55****	**5.09*****	3, 4 ,123	71, 06, 23
Gonad index	ASIN	ns	0.89ns	**9.23*****	3, 4 ,123	00, 28, 72
Diet composition	SQRT	***	**3.947****	**8.2437*****	3, 4 ,120	34, 21, 45
Trophic level	none	***	2.40ns	**164.02*****	3, 4, 122	39, 55, 06
Feeding behaviour Index	none	**	9.17*	**11.12*****	3, 4, 120	64, 14, 22

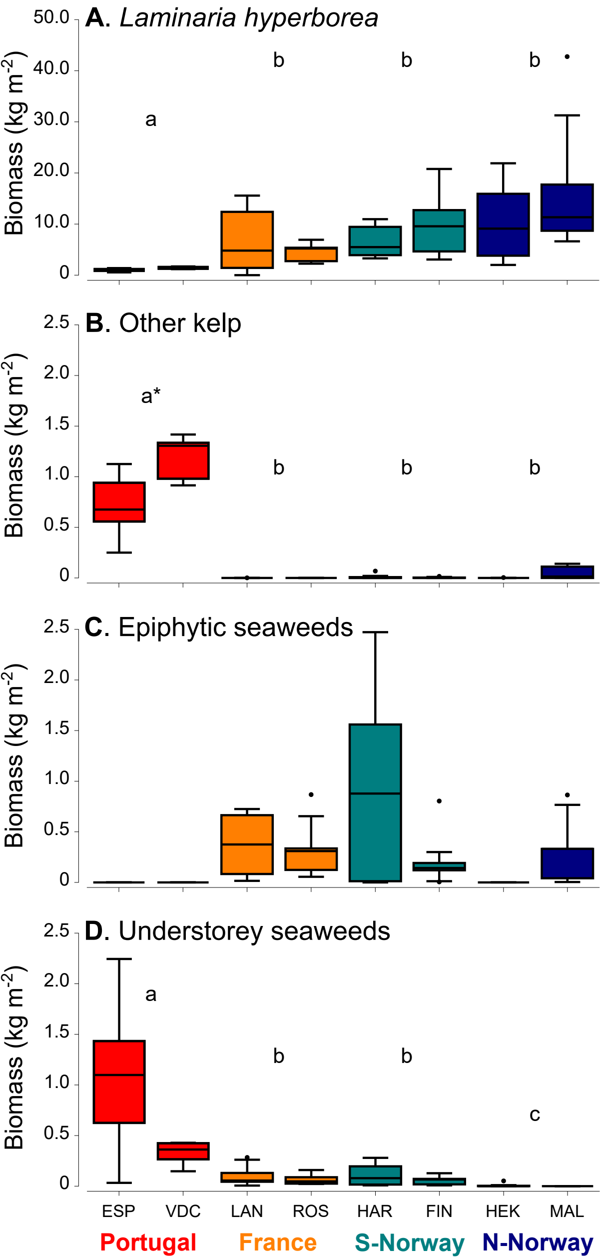
SQRT: Square root transformed, FORT: Fourth root transformed, ASIN: Arcsine transformed, LOG: Transformation Ln (X +1)

Figure 1. Mean biomass (kg m^{-2}) of kelp (A, B) and other seaweed categories (C, D) across study sites. Around the median (horizontal line), the box plots show the quartiles, the 95% confidence intervals (whiskers) and the outliers. Letters, superscript stars (*) indicate pair-wise differences ($P < 0.05$) among regions and among sites within regions, respectively. Note that the scale differs among panels.

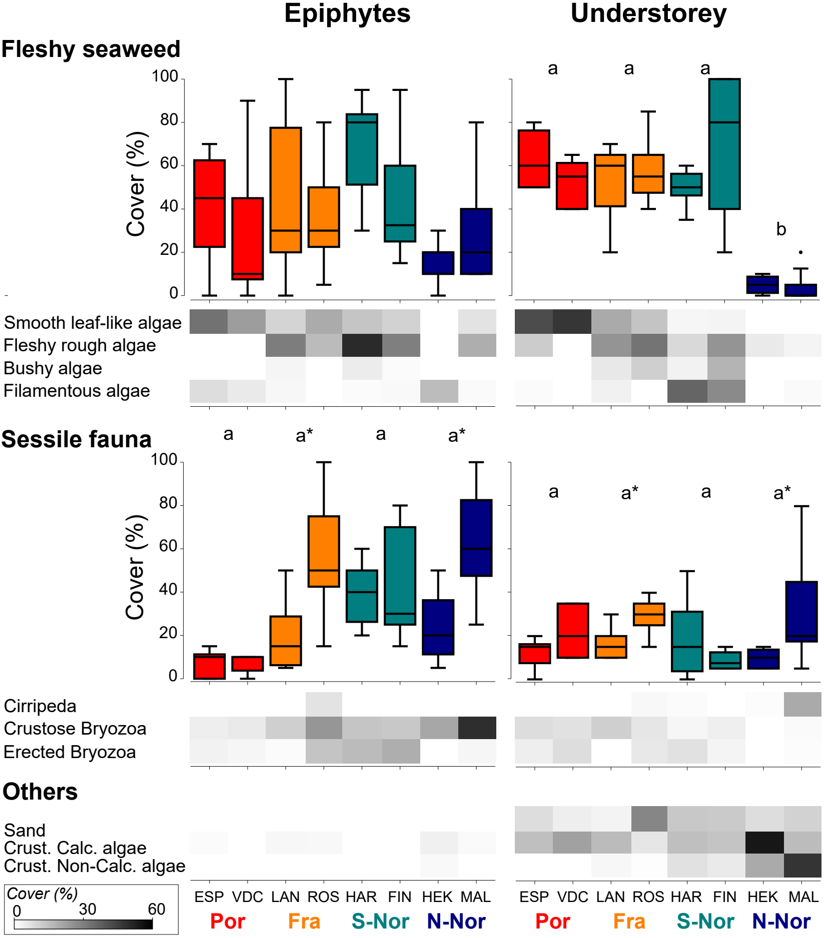
Figure 2. Fleshy seaweed (kelp and crustose algae excluded) and sessile fauna percentage cover (%) estimated upon stipe (epiphytes) and bedrock habitats (understory). The box plots show the total covers (with Q1, Median, Q3, 95% C.I.s and outliers). The heat maps illustrate the covers of the dominant morpho-functional groups (average SIMPER contribution > 5%) of fleshy seaweeds, sessile fauna and others. For each category, letters indicate differences among regions, within which superscript stars indicate differences among sites according to PERMANOVA pairwise tests.

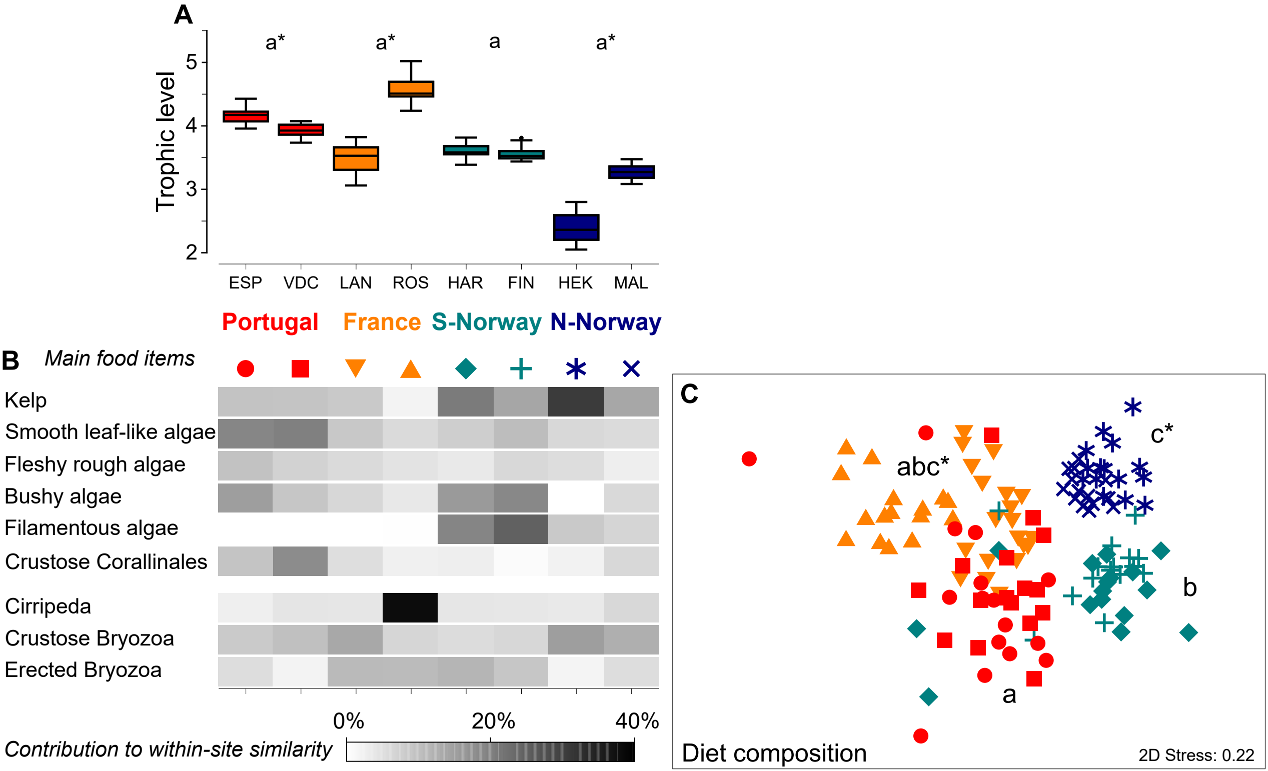
Figure 3. Trophic level (A), contribution of the main food items (B, average SIMPER contribution > 5%) to the diet composition (C) of *Echinus* within and across study sites. Around the median (horizontal line), the box plots show the quartiles, the 95% confidence intervals (whiskers) and the outlier. Letters and superscript stars indicate pair-wise differences among regions and among sites, respectively.

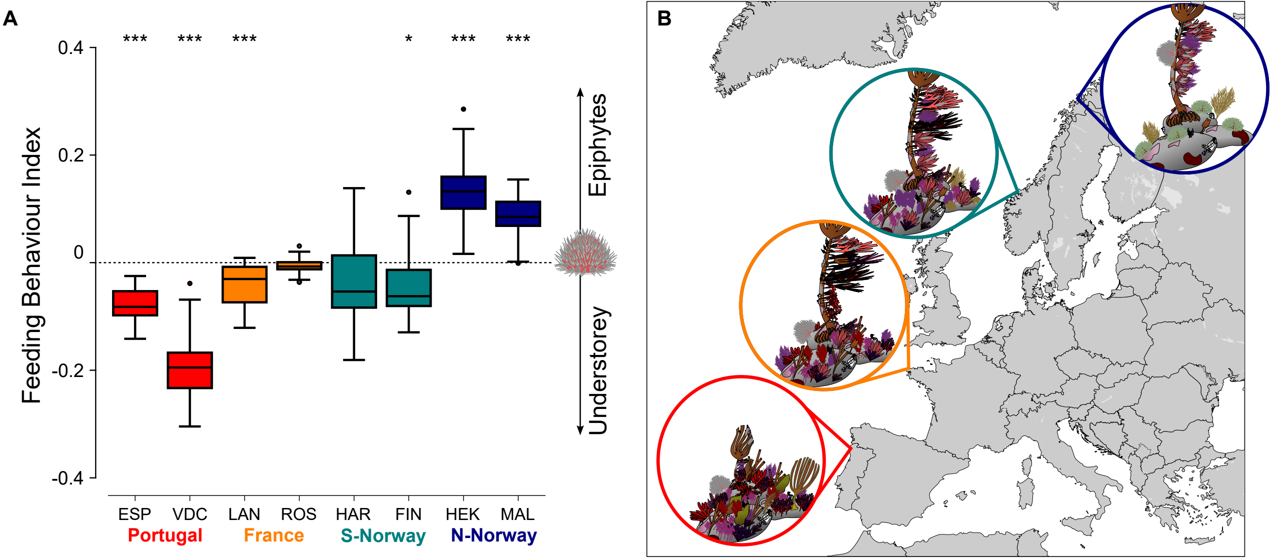
Figure 4. Feeding behaviour index (A) indicating affinities for epiphytes vs. understorey calculated from the functional similarities between *Echinus* diet and availability of food items (including seaweeds and fauna) upon kelp stipe and on the bedrock, and illustration of its meaning in the local context (B). Differences between the index values and 0 at the site level are summarized as follow: * = $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.



A. Laminaria hyperborea
B. Other kelp
C. Epiphytic seaweeds
D. Understorey seaweeds
Biomass (kg m-2)
0
10.0
20.0
30.0
40.0
50.0
0.5
1.0
1.5
2.0
2.5
a
b
a*
c
ESP
VDC
LAN
ROS
HAR
FIN
HEK
MAL
Portugal
France
S-Norway
N-Norway


Epiphytes
Understorey
Fleshy seaweed
Cover (%)
0
20
40
60
80
100
a
a
a
b
Smooth leaf-like algae
Fleshy rough algae
Bushy algae
Filamentous algae
Sessile fauna
a
a*
a
a*
a
a*
a
a*
Cirripeda
Crustose Bryozoa
Erected Bryozoa
Others
Sand
Crust. Calc. algae
Crust. Non-Calc. algae
Cover (%)
0
30
60
ESP
VDC
LAN
ROS
HAR
FIN
HEK
MAL
Por
Fra
S-Nor
N-Nor


A
Trophic level
2
3
4
5
a*
a*
a
a*
ESP
VDC
LAN
ROS
HAR
FIN
HEK
MAL
Portugal
France
S-Norway
N-Norway
B
Main food items
Kelp
Smooth leaf-like algae
Fleshy rough algae
Bushy algae
Filamentous algae
Crustose Corallinales
Cirripeda
Crustose Bryozoa
Erected Bryozoa
0%
20%
40%
Contribution to within-site similarity
C
abc*
c*
b
a
Diet composition
2D Stress: 0.22


A
***
***
***
*
***
***
Feeding Behaviour Index
0.4
0.2
0
-0.2
-0.4
Epiphytes
Understorey
ESP
VDC
LAN
ROS
HAR
FIN
HEK
MAL
Portugal
France
S-Norway
N-Norway
B