



HAL
open science

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

Jean-Charles Leclerc, Thibaut de Bettignies, Florian de Bettignies, Hartvig Christie, João N Franco, Cédric Leroux, Dominique Davoult, Morten F Pedersen, Karen Filbee-Dexter, Thomas Wernberg

► To cite this version:

Jean-Charles Leclerc, Thibaut de Bettignies, Florian de Bettignies, Hartvig Christie, João N Franco, et al.. Local flexibility in feeding behaviour and contrasting microhabitat use of an omnivore across latitudes. *Oecologia*, 2021, 196, pp.441-453. 10.1007/s00442-021-04936-5 . hal-03231854

HAL Id: hal-03231854

<https://hal.sorbonne-universite.fr/hal-03231854>

Submitted on 21 May 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3
4 Jean-Charles Leclerc^{1,2*}, Thibaut de Bettignies^{3,4}, Florian de Bettignies¹, Hartvig
5 Christie⁵, João N Franco^{6,7}, Cédric Leroux⁸, Dominique Davoult¹, Morten F.
6 Pedersen⁹, Karen Filbee-Dexter^{4,10}, Thomas Wernberg^{4,9,10}

7
8 ¹Sorbonne Université, CNRS, UMR 7144 AD2M, Station Biologique de Roscoff, Place Georges Teissier, 29680
9 Roscoff, France

10 ²Universidad Católica de la Santísima Concepción, Departamento de Ecología, Facultad de Ciencias, Centro de
11 Investigación en Biodiversidad y Ambientes Sustentables (CIBAS), Casilla 297, Concepción, Chile

12 ³UMS Patrimoine Naturel (PATRINAT), AFB-CNRS-MNHN, CP41, 36 rue Geoffroy Saint-Hilaire, 75005 Paris,
13 France

14 ⁴School of Biological Sciences & UWA Oceans Institute, University of Western Australia, 39 Fairway, Crawley
15 6009, WA, Australia.

16 ⁵Marine Biology Section, Norwegian Institute for Water Research, Oslo, Norway

17 ⁶CIIMAR, Terminal de Cruzeiros de Leixões. Av. General Norton de Matos, 4450-208 Matosinhos, Portugal

18 ⁷MARE—Marine and Environmental Sciences Centre, ESTM, Instituto Politécnico de Leiria, Peniche, Portugal

19 ⁸Sorbonne Université, CNRS, FR 2424, Station Biologique, Place Georges Teissier, 29680 Roscoff, France

20 ⁹Department for Science and Environment (DSE), Roskilde University, PO Box 260, 4000 Roskilde, Denmark

21 ¹⁰Benthic Communities Research Group, Institute of Marine Research, His, Norway

22
23 *leclercjc@gmail.com
24

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

31 **ABSTRACT**

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

49
50 **Key-words.** Food web, Opportunism, Trophic plasticity, Urchin grazing, *Laminaria hyperborea*,
51 *Echinus esculentus*

52

53 INTRODUCTION

54 Consumptive interactions (i.e., predation) can have major implications for the structure and
55 dynamics of communities (Chase et al. 2009; Vergés et al. 2019) and there are urgent needs for
56 determining their variations under changing climate and biodiversity redistribution (Sentis et al.
57 2014; Bruno et al. 2015; Rosenblatt and Schmitz 2016). In response to changes in prey abundances,
58 consumers can switch to alternative food items and/or readjust the strength of their interactions
59 with the prey (Sentis et al. 2014; Gilljam et al. 2015). In addition, and especially in the case of
60 ectotherms, some consumptive interactions can be strengthened due to changes in metabolic
61 requirements imposed by changing climate (Bruno et al. 2015; Rosenblatt and Schmitz 2016;
62 Anderson et al. 2017). The magnitude of these changes may, however, vary asymmetrically
63 between predators and prey depending on the differential thermal responses of both resource and
64 consumer traits, such as mobility and strategy to acquire resources (Dell et al. 2014). The diversity
65 of these scenarios is challenging predictions of future food webs and ecosystem functioning (Bruno
66 et al. 2015; Rosenblatt and Schmitz 2016; Kortsch et al. 2019; Vergés et al. 2019).

67 Latitudinal variation in species interactions has provided critical information on potential
68 future changes with climate warming (Wernberg et al. 2010; Bennett et al. 2015a; Vergés et al.
69 2019). Large scale comparative experiments from various habitats have strongly improved our
70 general understanding of both the structuring role of consumers on biodiversity gradients (Chase
71 et al. 2009; Freestone et al. 2011; Bennett et al. 2015b; Roslin et al. 2017; Whalen et al. in press)
72 and of the global evolutionary patterns of plant defences and plant-herbivore interactions (Pennings
73 and Silliman 2005; Demko et al. 2017). To our knowledge, however, only a few studies have
74 investigated intra-specific patterns in the activity of consumers across broad climatic gradients. In
75 their latitudinal comparison of the feeding behaviour of the isopod *Idotea balthica*, Bell and Sotka

76 (2012) revealed that this generalist grazer displayed local preferences for some of the food sources
77 available in different regions. In northeastern America, Anstett et al. (2014) compared the intensity
78 of grazing by different insects on the plant *Oenothera biennis* and observed every possible
79 relationship (positive, non-significant or negative) with increasing latitude, likely due to plant-
80 herbivore specialization (versus generalism) and herbivore traits. Whether local adaptation or
81 phenotypic plasticity is to be invoked, these two examples support the idea that the trophic position
82 of resident consumers can vary across spatial scales. Notwithstanding its pervasiveness, our current
83 understanding of omnivory (i.e. wherein a consumer feeds on several trophic levels) within taxa
84 across such scales remains highly limited (Clay et al. 2017).

85 There is a growing interest in understanding how omnivory varies with environmental
86 conditions, especially temperature, which has so far demonstrated mixed results (Rosenblatt and
87 Schmitz 2016; Anderson et al. 2017). The prevailing paradigm that the dietary proportion of
88 carbohydrates increases more than proteins with increasing temperature (because carbon-rich
89 compounds are more readily processed to meet energy demands via respiration), has received
90 experimental support from a range of different ectotherms (marine copepods, caterpillars,
91 freshwater crayfish, tadpoles and insect larvae; Croll and Watts 2004; Lee et al. 2015; Boersma et
92 al. 2016; Carreira et al. 2016). Out of three tadpole species tested by Carreira et al. (2016), however,
93 the most carnivorous species were incapacitated when fed macrophytes in warming conditions.
94 This last result contrasts with the paradigm and suggests that omnivory responses to temperature
95 may instead depend on initial species-specific diets (nutrient limitations), as also supported by
96 stoichiometric models (Anderson et al. 2017) (cf. Sperfeld et al. 2017 for further confrontation of
97 related theoretical frameworks). Increased consumption of protein over carbohydrates with
98 increasing temperature, in order to promote growth, development and survival, has been

99 experimentally shown in a grasshopper fed artificial diets (Schmitz et al. 2016) and more indirectly
100 (through varied C:N) in a beetle fed various plant species (Lemoine et al. 2013). Conversely, in
101 cold conditions, carbohydrate consumption may be enhanced to compensate for reduced energy
102 intake, as also suggested from experiments on the mealworm beetle fed synthetic diets (Rho and
103 Lee 2017). Based on such premises, it is of little surprise to find inconsistent seasonal variations in
104 omnivory across field studies (Miyasaka and Genkai-Kato 2009; Boersma et al. 2016), and calls
105 for additional comparative studies across multiple spatial scales and environments.

106 In this study, we examined the omnivory of a broadly distributed ectotherm consumer - the
107 sea urchin *Echinus esculentus* (hereafter *Echinus*) - across latitudes that are representative of
108 different climatic conditions. *Echinus* inhabits kelp forests along the latitudinal distribution of the
109 kelp *Laminaria hyperborea*, ranging from Portugal (~ 41°N) to northern Norway (71°N) (Tyler et
110 al. 1995). A substantially varied diet has generally been reported for the species, but has to the best
111 of our knowledge, never been compared across larger spatial scales and environments, in spite of
112 interesting patterns suggested by local-scale studies (see methods). Importantly, animal proteins
113 (and possibly lipids) are seemingly required in *Echinus*' diet to promote its somatic growth and
114 reproductive output (Bonsdorff and Vahl 1982; Kelly et al. 2001). This is also observed in other
115 sea urchins (e.g., Lares and McClintock 1991; Fernandez and Boudouresque 2000). In marine
116 systems, the amounts (per unit of dry mass) of proteins and lipids in sessile fauna are on average
117 3.2 and 5.5 times higher in than in seaweeds, which contain 3.9 times more carbohydrates than
118 fauna (Brey et al. 2010). Assuming the energy investment in foraging on the two food categories
119 is identical (both being sessile, Dell et al. 2014), we first hypothesized that (1) the sessile fauna
120 intake would be greater in warmer conditions, therefore producing an omnivory gradient across
121 latitudes. While absolute consumption rate could also vary with temperature (Bruno et al. 2015)

122 and thus counterbalance temperature-driven metabolic nutrient limitation (Anderson et al. 2017),
123 we also had the alternative hypothesis that (2) the balance between animal and algal food would
124 vary according to the local availability of food items, hence indicating an entirely opportunistic
125 behaviour uncoupled, at least directly, from climatic conditions. Should omnivory be driven by
126 opportunism, we further hypothesized that (3) the consumer would locally adjust its foraging
127 strategy at multiple spatial scales.

128

129 **METHODS**

130 Model species

131 Although the vast array of putative prey of *Echinus* is generally acknowledged and supported by
132 qualitative observations of gut contents made in Western Scotland (Comely and Ansell 1988;
133 Emson and Moore 1998), the Isle of Man (Moore 1934) and the English Channel (Leclerc et al.
134 2015), information regarding broad spatial variations in diet is generally lacking. Differences in
135 gonad condition across shallow and deep sites reported in previous studies have often been
136 attributed to contrasting diversity and availability of food items (Moore 1934; Nichols et al. 1985).
137 In addition, local-scale studies using stable isotopes have indicated that *Echinus* has a substantially
138 varied diet largely dominated by kelp in Norway (Fredriksen 2003) and by sessile fauna in France
139 (Leclerc et al. 2015). Whether these differences in diet reflect local response to available food
140 sources, changes relating to metabolic requirements or is incidental (e.g., as a function of different
141 temperature regimes) is unresolved.

142 Study sites and sampling

143 The sampling design consisted of four regions (separated by 1000s of kilometres), with two sites
144 (separated by 1-10s km) nested within each region. The study area ranged from northern Portugal
145 (41.6°N) to northern Norway (69.6°N), hence covering 28° of latitude (Table S1). Mean sea surface
146 temperatures (extracted from the Bio-Oracle database; Tyberghein et al. 2012; Assis et al. 2018 for
147 the period 2000-2014, Table S2) ranged from 7.0°C in northern Norway (average minimum and
148 maximum between 3.3 and 11.3°C) to 15.6°C in Portugal (between 13.0 and 18.2°C). Over the
149 same period, long-term temperature variations were weak in Portugal (range of ~ 5°C) and France
150 (6°C), under the direct influence of the Gulf Stream, moderate in northern Norway (8°C) and
151 comparatively greater in southern Norway (10°C). Each study site was haphazardly selected among
152 *Laminaria hyperborea* forests at a depth of 5-12 m below chart datum. Adult *Echinus* were
153 'frequent' (SACFOR scale) at all study sites (1-9 ind. 10 m⁻²). Within each study site, 16 to 20 sea
154 urchins, 6 young (stipe < ca. 5cm) and adult (stipe > ca. 5 cm) kelps were haphazardly collected
155 by divers, kept on ice and then processed in the laboratory within 12 hours. Within the framework
156 of distinct field campaigns, sampling was done in spring 2014 in France and southern Norway, in
157 spring 2015 in Portugal and in summer 2016 in northern Norway.

158 The abundance of primary producers and all potential urchin food sources (including sessile
159 fauna) were assessed using two distinct methods. At the site scale, the fleshy seaweed biomass (wet
160 weight: blotted with paper tissue and weighed) was determined at the lowest taxonomic level
161 possible (generally species) from destructively sampled 0.25 m² quadrats. In the laboratory,
162 seaweed biomass was further subdivided into two categories, either epilithic (on bedrock) or
163 epiphytic (on kelp stipe). In addition, a series of independent photos were taken to determine the
164 abundance of all potential food sources (including fauna) within the main strata of the kelp forest:
165 bedrock (n = 5-11) and stipe (n = 5-11). These potential food sources were classified using morpho-

166 functional groups of seaweeds and sessile fauna, which have proven relevant to address ecological
167 functions of complex stratified systems such as *Laminaria hyperborea* forests (see Appendix S1).
168 Percentage covers of morpho-functional groups of seaweeds and sessile fauna were visually
169 estimated by the same observer (JCL) from photos for each potential food source. These
170 estimations followed the Dethier et al. (1993) framework, by summing semi-abundance either over
171 sub-quadrats of the quadrats (0-4 × 25) or over linear (vertical) portions of the stipe (0-10 × 10).
172 Most fleshy seaweeds and their epiphytes (notably sessile fauna) were generally visible in photos,
173 making easier their abundance estimation easier. In both habitats, however, most understorey taxa
174 (crusts and small sessile fauna) or habitat features (sediment) could not be quantified and were thus
175 likely underestimated. While percentage cover were assessed with a fixed scale of 0.1 m² on the
176 bedrock, stipe area available to colonization by epiphytes varied across kelp individuals and was
177 not quantified. Nonetheless, differences in surface area (among stipes or between stipes and
178 quadrats) were not considered an issue in the context of our study since relative values of cover,
179 based on similar sampling intensity and broad functional groups (rather than species) were only
180 compared among these strata and gut contents (see section on data analyses).

181

182 Urchin diet and trophic position

183 In the laboratory, sea urchins were processed for a series of morphological parameters, such as
184 their size (maximum test width) and gonad index (ratio between gonad and total wet biomass).
185 Aristotle's lanterns and guts were dissected and stored in separate Ziploc bags at - 30°C until further
186 analysis. Unlike stable isotopes which give a time-integrative estimation of diet, gut contents give
187 a snapshot of feeding choices but are more robust to determine preferences and opportunism. Gut

188 contents also provide accurate information about prey species which have been ingested and are
189 therefore useful in determining individual habitat use and foraging strategies, within and among
190 sites (Vanderklift et al. 2006).

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

201 Stable isotope analyses were conducted on individual urchins and on the biomass-dominant
202 primary food source in order to estimate urchin trophic level. *Laminaria hyperborea* was expected
203 to be the most abundant fleshy seaweed (except in Portugal, see results) and the only seaweed
204 shared across all study sites. Within kelp forests, *L. hyperborea* also represents the dominant
205 trophic resource of sessile suspension-feeders (e.g. barnacles, bivalves, bryozoans), which can be
206 a major component of *Echinus* diet (Leclerc et al. 2013; 2015). Given these reasons and in the
207 absence of suspension-feeders isotope values (see also Post 2002) collected for this study, *L.*
208 *hyperborea* was chosen as baseline, using average $\delta^{15}\text{N}$ values of adult and young kelp individuals,
209 generally in the range of other seaweeds (Leclerc et al. 2013). Clean sections of kelp (ca. 4 \times 4 cm)

210 were dissected from newly-formed lamina on freshly collected adult kelp and around the meristem
211 (stipe and lamina) on young kelp. For *Echinus*, muscle tissues, reflecting time-integrative
212 assimilation of sources (e.g. Pinnegar and Polunin 1999), were dissected from the Aristotle's
213 lantern. Each sample was checked and when necessary cleaned from epiphytes using a scalpel,
214 thoroughly rinsed with filtered seawater, then oven-dried at 55°C for 48 h. Because $\delta^{15}\text{N}$ values
215 were targeted, no further treatment was deemed necessary. Dried samples were ground using an
216 agate mortar and a pestle, then put in tin capsules for mass-spectrometry analyses.

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

225

226 Data analyses

227 *Estimation of trophic level using stable isotopes*

228 Isotopic analyses helped to estimate trophic levels of each individual urchin ($\text{TL}_{\text{urchin}}$): $\text{TL}_{\text{urchin}} = 1$
229 $+ (\delta^{15}\text{N}_{\text{urchin}} - \delta^{15}\text{N}_{\text{baseline}}) / \text{DDDF}$, where $\delta^{15}\text{N}_{\text{baseline}}$ corresponds to the mean $\delta^{15}\text{N}$ of kelp
230 (averaged over adult and young kelps per site) and DDDF corresponds to diet-dependent

231 discrimination factor ($\Delta^{15}\text{N}$) calculated for each site according to Caut et al. (2009). This method
232 was chosen due to the omnivory of *Echinus* and given the large variability in kelp $\delta^{15}\text{N}$ observed
233 among sites (see also Figure S4). No discrimination factor has been proposed for sea urchins
234 (e.g., Vanderklift et al. 2006) and the use of a fixed $\delta^{15}\text{N}$ led to contradictory results in comparison
235 with gut contents analyses (overestimation of TL at sites where kelp were poorly enriched in ^{15}N).
236 In addition, dependency between diet $\delta^{15}\text{N}$ and discrimination factor has been experimentally
237 demonstrated in other echinoderms (Blanchet-Aurigny et al. 2012).

238

239 *Statistical analyses*

240 All univariate and multivariate data were analysed using the same two-way nested
241 PERMANOVAs, with 4999 permutations and the random factors 'region' and 'site'. Univariate
242 and multivariate analyses were respectively based on Euclidean distance and Bray-Curtis similarity
243 matrices. Univariate data included urchin size, gonad index and trophic level as well as the
244 abundances of the dominant groups of putative food items (biomass of kelp and other seaweeds,
245 percentage cover of seaweeds and sessile fauna), on either bedrock or stipe. Multivariate data
246 consisted of the relative abundances of each food item categories within gut contents. Prior to
247 analyses, the homogeneity in univariate or multivariate dispersion was checked among the levels
248 of the factor 'region' using PERMDISP (Anderson et al. 2008). When assumption of
249 homoscedasticity was not met after any transformation of univariate data, the analysis was
250 conducted on untransformed data following Underwood (1997) and a more conservative level of
251 significance ($\alpha = 0.01$) was taken into account. For multivariate structure, samples were also
252 ordinated using non-metric multidimensional scaling (nMDS) to support PERMANOVA results
253 (Anderson et al. 2008). In order to strengthen all these analyses, we also examined how the

254 variation was distributed across all three nested levels tested (region site, residual). When a
255 negative component of variations was found, it was set to zero and the model was adjusted in order
256 to re-calculate the remaining estimates (Fletcher and Underwood 2002).

257 Foraging strategies were determined from gut content similarities with prey distribution in
258 the sea urchin environment. At the site scale, the natural habitat-complexity of *L. hyperborea*
259 forests challenges the collection of abundance data for all possible food sources (Christie et al.
260 2003; Leclerc et al. 2016). More information can, however, be obtained from the abundances of
261 resource on two kelp forest strata known to be visited by *Echinus*: the understorey (on the bedrock)
262 and the epiphytes (on the stipe). We thus developed a relative and binary feeding behaviour index
263 for each of these two strata. First, abundance (cover) data of the main food item categories (except
264 kelp) in different habitats (bedrock and stipe) and within urchin guts were all compiled in a unique
265 matrix. We did not include kelp in the analyses because they were often observed in the urchin diet
266 as a varying mixture of fragment types (ranging from a relative scale of soft to hard tissues, with
267 or without cortex, etc.), which could hardly be assigned to understorey or stipe. Indeed, these
268 diverse type of tissues can be found in varying abundances within either canopy kelp individuals
269 (Kain 1963), understorey young individuals, or detritus (Filbee-Dexter et al. 2018). Second, a
270 matrix of dissimilarity between all pairs of samples was created using the Bray-Curtis index
271 calculated from untransformed data. Third, for each site, principal coordinates were calculated
272 from the Bray-Curtis dissimilarity (non-metric) matrices in order to extract Euclidean distances
273 (metric) between all pairs of samples, while preserving the properties of the Bray-Curtis index.
274 Fourth, for each individual urchin, the average distance between its diet and the food item
275 abundances in each of its putatively targeted habitats (stipe or bedrock) was then calculated. Fifth,
276 the relative and binary feeding behaviour index (FBI) was subsequently calculated for each

277 individual, based upon Armas et al. (2004), as follow: $FBI = (D_{d-h1} - D_{d-h2}) / (D_{d-h1} + D_{d-h2})$, where
278 D_{d-h1} = multivariate distance between individual diet and the habitat 1 (here bedrock) and D_{d-h2} =
279 distance between individual diet and the habitat 2 (stipe). This FBI presents a continuous scale and
280 ranges between -1 and $+1$ indicating a marked (and theoretical) affinity for habitats 1 and 2,
281 respectively. Finally, in order to determine whether urchins present a significant “preference” for
282 one habitat or another at the local scale, PI values were compared to 0 using one-sample *t*-tests
283 within each site. The latter analysis was performed using SigmaPlot, while PERMANOVAs,
284 nMDS and PERMDISPs were performed using PRIMER 7 with PERMANOVA add-on (Anderson
285 et al. 2008).

286

287 **RESULTS**

288 Across sites and regions, a total of 131 sea urchins were analysed and presented consistent regional
289 differences in both size (test diameter) and wet weight (ww) between core (France, southern
290 Norway) and edge (Portugal, northern Norway) regions (Table 1, Fig. S1). Sea urchins were
291 significantly smaller in Portugal (85.3 ± 7.4 mm, mean \pm SD) and northern Norway (78.1 ± 12.3
292 mm) than in France (113.3 ± 10.1 mm) and southern Norway (110.8 ± 15.7 mm). Likewise, and in
293 spite of within-region significant effects, sea urchins were three times lighter (85.3 ± 7.4 g_{ww}) in
294 Portugal (274.4 ± 62.5 g_{ww}) and northern Norway (224.6 ± 107.6 g_{ww}) than in France ($778.3 \pm$
295 222.8 g_{ww}) and southern Norway (673.5 ± 217.3 g). Their gonad index varied substantially within
296 sites (72% of variation due to residuals in the model, Table 1) but did not vary among regions (on

297 average 7.2 ± 4.04 , Fig. S1). Interestingly though, this index displayed significant site-to-site
298 differences in both Portugal and northern Norway (Table 1, Fig. S1).

299 *Contrasting patterns in food availability at multiple spatial scales*

300 Food availability varied markedly across different spatial scales (among regions, sites, micro-
301 habitats), and depended on food type. *Laminaria hyperborea* dominated the seaweed biomass from
302 France ($5.6 \pm 4.5 \text{ kg}_{\text{ww}} \text{ m}^{-2}$, mean \pm SD) to northern Norway ($13.7 \pm 11.3 \text{ kg}_{\text{ww}} \text{ m}^{-2}$, Fig. 1A, Table
303 1), where similar values were observed, but its biomass was much lower ($< 0.1 \text{ kg}_{\text{ww}} \text{ m}^{-2}$) in
304 Portugal, where the canopy was dominated by the pseudo-annual kelp *Sacchoriza polyschides* (0.9
305 $\pm 0.3 \text{ kg}_{\text{ww}} \text{ m}^{-2}$, Fig. 1B). The epiphyte biomass was statistically similar among regions (Fig. 1C,
306 Table 1), and highly variable within and among sites (cf. %var. in Table 1). It is noteworthy that
307 epiphyte biomass was virtually zero at all sites in Portugal and at the Hekkingen site (cf. Table S1)
308 in northern Norway. Significant regional differences were detected for the understory biomass
309 (Fig. 1D). In northern Norway, the fleshy algal understory was patchy, monospecific
310 (*Desmarestia aculeata* and the biomass was negligible ($5.1 \pm 15.6 \text{ g}_{\text{ww}} \text{ m}^{-2}$) when compared to
311 other regions (Table 1, Fig. 1D). Understorey biomass was similar in France ($80.4 \pm 78.1 \text{ g}_{\text{ww}} \text{ m}^{-2}$)
312 and southern Norway ($84.6 \pm 831 \text{ g}_{\text{ww}} \text{ m}^{-2}$) and about ten-fold lower than in Portugal (775.9 ± 665.5
313 $\text{g}_{\text{ww}} \text{ m}^{-2}$, Table 1, Fig. 1D). Similar spatial patterns were shown when fleshy seaweeds were
314 quantified using percentage cover with only the epilithic algae differing significantly between
315 northern Norway ($10.0 \pm 7.1\%$, dominated by crusts, Fig. 2) and the other regions (on average 55.9
316 $\pm 16.1\%$, Table 1, Fig. 2). In contrast, neither the percent cover of sessile fauna associated with the
317 stipes or with the bedrock differed among regions, but both displayed substantial site-to-site
318 variations in France and northern Norway (Table 1, Fig. 2).

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

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

331

332 *Adjustment of foraging strategy at multiple spatial scales*

333 Analysing the similarity between the generalist diet and the distribution of its putative food items
334 proved efficient to infer spatial patterns in foraging strategies in space, here between two kelp forest
335 strata: the bedrock and the stipe (Fig. 4). Although broad groups of sessile taxa were considered,
336 the community (or functional) structure of these strata differed significantly within and across study
337 sites (Table S3, Fig. S2). Based on these cover data, sea urchins displayed significant net affinity
338 for one habitat or another in 6 out of the total 8 sites (Fig. 4). Within regions, consistent affinities
339 for the understorey habitats were observed in Portugal whereas consistent affinities for the epiphyte

340 habitats were found in northern Norway. Site-specific affinities for the understory were also
341 observed in France and southern Norway (cf. also site within region effect, Table 1), but it is
342 noteworthy that many individuals (15.5%) from southern Norway displayed a net affinity for the
343 epiphytes (PI ranging from + 0.05 to + 0.18, Fig. 4A).

344

345 **DISCUSSION**

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

356

357 *Consistent omnivory across latitudes*

358 Metabolic scaling theory (Bruno et al. 2015), the foraging strategy towards sessile prey (Dell et al.
359 2014) and previous published diets of *Echinus* from local studies (Fredriksen 2003; Leclerc et al.
360 2015) suggest that animal (protein rich) food intake of this sea urchin should decrease with ocean
361 warming, and therefore with increasing latitude. Although we do not provide evidence on possible

362 individual diet adjustments with temperature (within populations), the latitudinal hypothesis
363 (among populations) is generally rejected by this study. By analysing both gut contents and stable
364 isotopes, our results indicate that *Echinus* maintains omnivory (algal versus animal contribution to
365 the diet) across its latitudinal range. Should temperatures experienced by the sea urchin across its
366 latitudinal range have any influence on its metabolic requirements, our results would align best
367 with models in which stoichiometric imbalance, and dietary preferences, can be preserved by
368 overall increased intake with temperature (Anderson et al. 2017). While temperature is most likely
369 to affect per capita interaction strength, it does not seem to affect *Echinus* food preference at the
370 latitudinal scale studied. Diverse groups of algae and animals were consistently identified as part
371 of the urchin diet at all study sites (e.g. bryozoans, barnacles, kelp and fleshy seaweeds) and nothing
372 indicated a latitudinal shift in their respective abundance. Using stable isotopes ($\delta^{15}\text{N}$), estimates
373 of trophic level generally aligned with the relative abundance of food items in digestive contents
374 and previous local studies. For instance, the highest trophic level (4.6 ± 0.2) observed in Roscoff
375 (France) is consistent with Leclerc et al. (2015) estimations in a nearby locality (TL = 4.0), wherein
376 a similar diet was observed. The lowest trophic level (2.4 ± 0.2) estimated in Hekkingen (northern
377 Norway) was also consistent with a kelp-dominated diet shown by gut content analyses. While the
378 trophic level was consistent across regions, it varied markedly among sites within region, providing
379 support to alternative hypotheses, notably related with food availability (see following sections).

380

381 *Omnivory reflects local food availability across multiple spatial scales*

382 The overall site-to-site variability in both $\delta^{15}\text{N}$ and gut contents suggests that spatial patterns
383 in omnivory may be driven mainly by opportunism (in response to food availability) as opposed to

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

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

417 At the southern (warm) edge of *Laminaria hyperborea* distribution (Portugal), kelp were
418 reduced to small individuals with little to no epiphytes, and there was virtually no stratification
419 (i.e., canopy/sub-canopy) of the kelp forests. In the same region, our index revealed a net affinity
420 for the understory, where the seaweed biomass was concentrated (Fig. 3B, Fig. S3) and included
421 the few species observed on the stipe (e.g. *Rhodymenia* sp.). Range centre populations of *Echinus*
422 in France and southern Norway were in different kelp forest conditions compared to Portugal, and
423 had access to both epiphytes and understory seaweeds. *Laminaria hyperborea* forests were similar
424 within and between these two regions, with the prevalence of large kelp individuals (main biomass)
425 loaded by abundant epiphytes (including kelp). The same sites in France and southern Norway
426 were also accompanied by diverse seaweeds and sessile animals growing on the surrounding
427 bedrock. In these kelp forests, our feeding behaviour index suggests that *Echinus* can encounter
428 most of the needed food items in the understory habitat, although net affinities for either habitat

429 were not significant at two of these sites (Fig. 4). These patterns contrast with northern Norway,
430 where a net affinity for epiphytes was observed. Although abundant epiphytes were found at one
431 site, the understory habitat at both these sites was generally depauperate and mainly covered by
432 crustose seaweeds, when compared to other regions. If food becomes limited in the understory,
433 climbing up kelp stipes is probably the best way for a sea urchin to diversify its diet (Bekkby et al.
434 2015). Consumers venturing on the upper part of stipe can actually access *Palmaria palmata*, which
435 is probably the most palatable red seaweed in the subtidal NE Atlantic kelp forests (Guiry and
436 Blunden 1991; Schaal et al. 2010). Commonly encrusted by the bryozoan *Electra pilosa*, *P.*
437 *palmata* was herein observed in varying abundance as (and only as) epiphytes from France to
438 northern Norway, and this combination of food items made up the entire diet of some individuals
439 from several of the studied localities (JCL, pers. obs.). Further work would be needed to determine
440 the prevalence of possible individual preferences within the sea urchin populations. More
441 interestingly, it is worth noting that *Echinus* is coexisting with *Strongylocentrotus droebachiensis*
442 (at densities of ca. 0.5 to 1.2 m⁻², Filbee-Dexter et al. 2020) in northern Norway. Should that
443 voracious sea urchin be involved in the control of understory algae (cf. Christie et al. 2019 and
444 references therein), our feeding behaviour index would thus mirror that competition for food
445 resource affect the foraging flexibility of *Echinus*, and force it to browse another habitat (Fig. 4B).
446 This point deserves further attention.

447

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

450 While the importance of habitat-forming species, such as kelp, for biodiversity is generally
451 acknowledged, it is noteworthy that not all kelp species share the same habitat-forming traits (e.g.
452 Wernberg et al. 2019 and references therein). Compared to other kelp, the stipe of *L. hyperborea*
453 possess a series of traits conducive to colonization by abundant perennial and semi-annual
454 epiphytes (reviewed in Teagle and Smale 2018), within which diverse and abundant assemblages
455 of fauna can develop and fuel local and adjacent food webs (Norderhaug et al. 2005; Leclerc et al.
456 2013). Across diverse taxa or morpho-functional groups, sessile epiphytes are indeed characterized
457 by varied structural complexity which have been shown to influence macrofaunal diversity and
458 community structure, at multiple spatial scales (Norderhaug 2004; Norderhaug et al. 2014). A
459 single stipe of kelp can be inhabited by up to 85 macrofaunal species (Leclerc et al. 2016), with
460 abundances that can exceed 80,000 individuals (Christie et al. 2003) and may constitute a
461 microscale diversity refuge in disturbed areas (Leclerc et al. 2015). Although the present data do
462 not provide quantitative evidence for urchin-epiphyte interactions, they align with Bekkby et al.
463 (2015) who demonstrated that *Echinus* can significantly reduce the abundance of kelp epiphytes in
464 mid-Norway, and thus alter the function of this microhabitat. Interestingly, those authors observed
465 a stronger control of epiphytes in ‘young’ kelp forests undergoing a process of recolonization post-
466 overgrazing by *Strongylocentrotus droebachiensis*, compared to *Echinus*, which were likely more
467 limited by food availability. The paucity of understorey seaweeds in northern Norway as compared
468 to other regions, regardless of the underlying processes (light limitation, grazing by *S.*
469 *droebachiensis*), is thus likely to exacerbate *Echinus* effects upon the diversity and community
470 structure at local scale in these kelp forests.

471 Kelp was a minor component of the sea urchin diet at all but one site. Kelp contributed to
472 30.6% at the northernmost site (Hekkingen, northern Norway), where alternative food items were

473 poorly represented. The most probable explanation for this pattern is that *Echinus* switches to a
474 kelp-dominated diet only when other food items are limited (even epiphytes were virtually absent
475 locally). This has been seen in previous studies conducted in both UK and Norway: negative effects
476 of *Echinus* on kelp – and more specifically recruits – are generally observed in “transition” areas,
477 including the lower vertical (i.e. depth) distribution limit of kelp (Jones and Kain 1967), overgrazed
478 areas (Hagen 1983), and localities or patches undergoing a recovery post-harvesting (Steen et al.
479 2016). On the other hand, our results revealed that kelp presented similar contributions to the urchin
480 diet in Portugal as compared to other regions, although their biomass in the urchin habitat was ten-
481 fold lower. Even as a minor component, kelp are rich in carbohydrates and may actually be essential
482 to the mixed diet of the sea urchin. Whether the stronger effect of *Echinus* on kelp observed in
483 transition areas and lower depth limit can hold for the southern edge of *L. hyperborea* distribution
484 may be worthy of further investigation (Fig. 4).

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

493

494 **Acknowledgements.** We thank all the people who assisted with diving and logistics at the different
495 localities: L. Lévêque, Y. Fontana, M. Camusat, W. Thomas, N. Guidal and F. Le Ven in Roscoff
496 (Marine operations staff, SBR), N. L. Frisk in Tromsø (Roskilde University, KELPEX). We are
497 grateful to M. Thiel and two anonymous reviewers, whose comments helped substantially to
498 improve the manuscript. JCL further thanks the Centre IDEAL (Investigación Dinámica de
499 Ecosistemas Marinos de Altas Latitudes, Universidad Austral de Chile) for kind hospitality over
500 the manuscript preparation. Funding for this work was provided by the Australian Research
501 Council (TW: FT110100174, TW, KFD: DP190100058), the University of Western Australia
502 Research Collaboration Awards (TW, TdB, JCL, DD, JNF, HC), the France-Australia Science
503 Innovation Collaboration 2014 program (TdB, TW, JCL, DD), Metabomer and Corsaire Core
504 Facility (CL), the French Government run by the National Research Agency with regards to the
505 investment expenditure programme IDEALG ANR-10-BTBR-04 (JCL, DD) and the Norwegian
506 Research Council (TW, MFP, KFD, KELPEX 255085/E40).

507
508 **Data accessibility:** Most of the data are provided in the supplementary material associated with
509 the manuscript. Detailed data are available from the corresponding author upon reasonable request.

510

511

512

513 **References**

- 514
- 515 Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: Guide to Software
516 and Statistical Methods. PRIMER-E: Plymouth UK.
- 517 Anderson TR, Hessen DO, Boersma M, Urabe J, Mayor DJ (2017) Will invertebrates require
518 increasingly carbon-rich food in a warming world? *The American Naturalist* 190:725-742
- 519 Anstett DN, Naujokaitis-Lewis I, Johnson MT (2014) Latitudinal gradients in herbivory on
520 *Oenothera biennis* vary according to herbivore guild and specialization. *Ecology* 95:2915-
521 2923
- 522 Armas C, Ordiales R, Pugnaire FI (2004) Measuring plant interactions: a new comparative index.
523 *Ecology* 85:2682-2686
- 524 Assis J, Tyberghein L, Bosch S, Verbruggen H, Serrão EA, De Clerck O (2018) Bio-ORACLE
525 v2.0: Extending marine data layers for bioclimatic modelling. *Global Ecology and*
526 *Biogeography* 27:277-284
- 527 Bekkby T, Angeltveit G, Gundersen H, Tveiten L, Norderhaug KM (2015) Red sea urchins
528 (*Echinus esculentus*) and water flow influence epiphytic macroalgae density. *Marine*
529 *Biology Research* 11:375-384
- 530 Bell TM, Sotka EE (2012) Local adaptation in adult feeding preference and juvenile performance
531 in the generalist herbivore *Idotea balthica*. *Oecologia* 170:383-393
- 532 Bennett S, Wernberg T, de Bettignies T, Kendrick GA, Anderson RJ, Bolton JJ, Rodgers KL,
533 Shears NT, Leclerc J-C, Lévêque L, Davoult D, Christie HC (2015a) Canopy interactions
534 and physical stress gradients in subtidal communities. *Ecology Letters* 18:677-686
- 535 Bennett S, Wernberg T, Harvey ES, Santana-Garcon J, Saunders BJ (2015b) Tropical herbivores
536 provide resilience to a climate-mediated phase shift on temperate reefs. *Ecology Letters*
537 18:714-723
- 538 Blanchet-Aurigny A, Guillou M, Pernet F, Gaffet J-D, Dubois SF (2012) Tissue-diet discrimination
539 factors of isotopic ratios ($\Delta\delta^{13}\text{C}$ and $\Delta\delta^{15}\text{N}$) in two brittle star species: Effect of reproductive
540 state, diet and tissue composition. *Journal of Experimental Marine Biology and Ecology*
541 426:68-77
- 542 Boersma M, Mathew KA, Niehoff B, Schoo KL, Franco-Santos RM, Meunier CL (2016)
543 Temperature driven changes in the diet preference of omnivorous copepods: no more meat
544 when it's hot? *Ecology letters* 19:45-53
- 545 Bonsdorff E, Vahl O (1982) Food preference of the sea urchins *Echinus acutus* and *E. esculentus*.
546 *Marine Behaviour and Physiology* 8:243-248
- 547 Brey T, Müller-Wiegmann C, Zittier ZMC, Hagen W (2010) Body composition in aquatic
548 organisms - A global data bank of relationships between mass, elemental composition and
549 energy content. *Journal of Sea Research* 64:334-340
- 550 Bruno JF, Carr LA, O'Connor MI (2015) Exploring the role of temperature in the ocean through
551 metabolic scaling. *Ecology* 96:3126-3140
- 552 Camps-Castellà J, Romero J, Prado P (2020) Trophic plasticity in the sea urchin *Paracentrotus*
553 *lividus*, as a function of resource availability and habitat features. *Marine Ecology Progress*
554 *Series* 637:71-85
- 555 Carreira B, Segurado P, Orizaola G, Gonçalves N, Pinto V, Laurila A, Rebelo R (2016) Warm
556 vegetarians? Heat waves and diet shifts in tadpoles. *Ecology* 97:2964-2974

- 557 Caut S, Angulo E, Courchamp F (2009) Variation in discrimination factors ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$): the
558 effects of diet isotopic values and applications for diet reconstruction. *Journal of Applied*
559 *Ecology* 46:443-453
- 560 Chase JM, Biro EG, Ryberg WA, Smith KG (2009) Predators temper the relative importance of
561 stochastic processes in the assembly of prey metacommunities. *Ecology Letters* 12:1210-
562 1218
- 563 Christie H, Gundersen H, Rinde E, Filbee-Dexter K, Norderhaug KM, Pedersen T, Bekkby T,
564 Gitmark JK, Fagerli CW (2019) Can multitrophic interactions and ocean warming influence
565 large-scale kelp recovery? *Ecology and Evolution* 9:2847-2862
- 566 Christie H, Jørgensen NM, Norderhaug KM, Waage-Nielsen E (2003) Species distribution and
567 habitat exploitation of fauna associated with kelp (*Laminaria hyperborea*) along the
568 Norwegian coast. *Journal of the Marine Biological Association of the United Kingdom*
569 83:687-699
- 570 Clay NA, Lehrter RJ, Kaspari M (2017) Towards a geography of omnivory: Omnivores increase
571 carnivory when sodium is limiting. *Journal of Animal Ecology* 86:1523-1531
- 572 Comely CA, Ansell AD (1988) Population density and growth of *Echinus esculentus* L. on the
573 Scottish west coast. *Estuarine, Coastal and Shelf Science* 27:311-334
- 574 Croll SL, Watts SA (2004) The effect of temperature on feed consumption and nutrient absorption
575 in *Procambarus clarkii* and *Procambarus zonangulus*. *Journal of the World Aquaculture*
576 *Society* 35:478-488
- 577 Dell AI, Pawar S, Savage VM (2014) Temperature dependence of trophic interactions are driven
578 by asymmetry of species responses and foraging strategy. *Journal of Animal Ecology*
579 83:70-84
- 580 Demko AM, Amsler CD, Hay ME, Long JD, McClintock JB, Paul VJ, Sotka EE (2017) Declines
581 in plant palatability from polar to tropical latitudes depend on herbivore and plant identity.
582 *Ecology* 98:2312-2321
- 583 Dethier MN, Graham ES, Cohen S, Tear LM (1993) Visual versus random-point percent cover
584 estimations: 'objective' is not always better. *Marine Ecology Progress Series* 96:93-100
- 585 Emson RH, Moore PG (1998) Diet and gonad size in three populations of *Echinus esculentus*. In:
586 Mooi R, Telford M (eds) *Echinoderms*: San Francisco. Balkema, Rotterdam, pp 641-644
- 587 Fernandez C, Boudouresque C-F (2000) Nutrition of the sea urchin *Paracentrotus lividus*
588 (Echinodermata: Echinoidea) fed different artificial food. *Marine Ecology Progress Series*
589 204:131-141
- 590 Filbee-Dexter K, Pedersen MF, Fredriksen S, Norderhaug KM, Rinde E, Kristiansen T, Albreten
591 J, Wernberg T (2020) Carbon export is facilitated by sea urchins transforming kelp detritus.
592 *Oecologia* 192:213-225
- 593 Filbee-Dexter K, Wernberg T, Norderhaug KM, Ramirez-Llodra E, Pedersen MF (2018)
594 Movement of pulsed resource subsidies from kelp forests to deep fjords. *Oecologia*
595 198:291-304
- 596 Fletcher D, Underwood A (2002) How to cope with negative estimates of components of variance
597 in ecological field studies. *Journal of Experimental Marine Biology and Ecology* 273:89-
598 95
- 599 Fredriksen S (2003) Food web studies in a Norwegian kelp forest based on stable isotope ($\delta^{13}\text{C}$ and
600 $\delta^{15}\text{N}$) analysis. *Marine Ecology Progress Series* 260:71-81
- 601 Freestone AL, Osman RW, Ruiz GM, Torchin ME (2011) Stronger predation in the tropics shapes
602 species richness patterns in marine communities. *Ecology* 92:983-993

603 Gilljam D, Curtsdotter A, Ebenman B (2015) Adaptive rewiring aggravates the effects of species
604 loss in ecosystems. *Nature Communications* 6:8412

605 Guiry MD, Blunden G (1991) *Seaweed resources in Europe: uses and potential*, Chichester

606 Hagen NT (1983) Destructive grazing of kelp beds by sea urchins in Vestfjorden, Northern
607 Norway. *Sarsia* 68:177-190

608 Jones NS, Kain JM (1967) Subtidal algal colonization following the removal of *Echinus*. *Helgoland*
609 *Marine Research* 15:460-466

610 Kain-Jones JM (1971) Synopsis of biological data on *Laminaria hyperborea*. *FAO Fisheries*
611 *synopsis* 87

612 Kain JM (1963) Aspects of the Biology of *Laminaria hyperborea* II. Age, weight and length.
613 *Journal of the Marine Biological Association of the United Kingdom* 43:129-151

614 Kelly MS, Owen PV, Pantazis P (2001) The commercial potential of the common sea urchin
615 *Echinus esculentus* from the west coast of Scotland. *Hydrobiologia* 465:85-94

616 Kortsch S, Primicerio R, Aschan M, Lind S, Dolgov AV, Planque B (2019) Food-web structure
617 varies along environmental gradients in a high-latitude marine ecosystem. *Ecography*
618 42:295-308

619 Lares MT, McClintock JB (1991) The effects of food quality and temperature on the nutrition of
620 the carnivorous sea urchin *Eucidaris tribuloides* (Lamarck). *Journal of Experimental*
621 *Marine Biology and Ecology* 149:279-286

622 Leclerc J-C, Riera P, Laurans M, Leroux C, Lévêque L, Davoult D (2015) Community, trophic
623 structure and functioning in two contrasting *Laminaria hyperborea* forests. *Estuarine,*
624 *Coastal and Shelf Science* 152:11-22

625 Leclerc J-C, Riera P, Leroux C, Lévêque L, Davoult D (2013) Temporal variation in organic matter
626 supply in kelp forests: linking structure to trophic functioning. *Marine Ecology Progress*
627 *Series* 494:87-105

628 Leclerc J-C, Riera P, Lévêque L, Davoult D (2016) Contrasting temporal variation in habitat
629 complexity and species abundance distributions in four kelp forest strata. *Hydrobiologia*
630 777:33-54

631 Lee KP, Jang T, Ravzanaadii N, Rho MS (2015) Macronutrient balance modulates the temperature-
632 size rule in an ectotherm. *The American Naturalist* 186:212-222

633 Lemoine NP, Drews WA, Burkepile DE, Parker JD (2013) Increased temperature alters feeding
634 behavior of a generalist herbivore. *Oikos* 122:1669-1678

635 Minor MA, Scheibling RE (1997) Effects of food ration and feeding regime on growth and
636 reproduction of the sea urchin *Strongylocentrotus droebachiensis*. *Marine Biology*
637 129:159-167

638 Miyasaka H, Genkai-Kato M (2009) Shift between carnivory and omnivory in stream stonefly
639 predators. *Ecological research* 24:11-19

640 Moore HB (1934) A comparison of the biology of *Echinus esculentus* in different habitats. *Journal*
641 *of the Marine Biological Association of the United Kingdom* 19:869-885

642 Nichols D, Bishop GM, Sime AAT (1985) Reproductive and nutritional periodicities in populations
643 of the European sea-urchin, *Echinus Esculentus* (Echinodermata: Echinoidea) from the
644 English Channel. *Journal of the Marine Biological Association of the United Kingdom*
645 65:203-220

646 Norderhaug KM (2004) Use of red algae as hosts by kelp-associated amphipods. *Marine Biology*
647 144:225-230

648 Norderhaug KM, Christie H, Fossa JH, Fredriksen S (2005) Fish-macrofauna interactions in a kelp
649 (*Laminaria hyperborea*) forest. Journal of the Marine Biological Association of the United
650 Kingdom 85:1279-1286

651 Norderhaug KM, Christie H, Rinde E, Gundersen H, Bekkby T (2014) Importance of wave and
652 current exposure to fauna communities in *Laminaria hyperborea* kelp forests. Marine
653 Ecology Progress Series 502:295-301

654 Paul D, Skrzypek G, Fórizs I (2007) Normalization of measured stable isotopic compositions to
655 isotope reference scales—a review. Rapid Communications in Mass Spectrometry: An
656 International Journal Devoted to the Rapid Dissemination of Up-to-the-Minute Research in
657 Mass Spectrometry 21:3006-3014

658 Pennings SC, Silliman BR (2005) Linking biogeography and community ecology: latitudinal
659 variation in plant–herbivore interaction strength. Ecology 86:2310-2319

660 Pinnegar JK, Polunin NVC (1999) Differential fractionation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among fish tissues:
661 implications for the study of trophic structure. Functional Ecology 13:225-231

662 Post D (2002) Using stable isotopes to estimate trophic positions: models, methods, and
663 assumptions. Ecology 83:703-718

664 Rho MS, Lee KP (2017) Temperature-driven plasticity in nutrient use and preference in an
665 ectotherm. Oecologia 185:401-413

666 Rosenblatt AE, Schmitz OJ (2016) Climate change, nutrition, and bottom-up and top-down food
667 web processes. Trends in ecology & evolution 31:965-975

668 Roslin T, Hardwick B, Novotny V, Petry WK, Andrew NR, Asmus A, Barrio IC, Basset Y, Boesing
669 AL, Bonebrake TC, Cameron EK, Dáttilo W, Donoso DA, Drozd P, Gray CL, Hik DS, Hill
670 SJ, Hopkins T, Huang S, Koane B, Laird-Hopkins B, Laukkanen L, Lewis OT, Milne S,
671 Mwesige I, Nakamura A, Nell CS, Nichols E, Prokurat A, Sam K, Schmidt NM, Slade A,
672 Slade V, Suchanková A, Teder T, van Nouhuys S, Vandvik V, Weissflog A, Zhukovich V,
673 Slade EM (2017) Higher predation risk for insect prey at low latitudes and elevations.
674 Science 356:742-744

675 Schaal G, Riera P, Leroux C (2010) Trophic ecology in a Northern Brittany (Batz Island, France)
676 kelp (*Laminaria digitata*) forest, as investigated through stable isotope and chemical assays.
677 Journal of Sea Research 63:24-35

678 Schmitz OJ, Rosenblatt AE, Smylie M (2016) Temperature dependence of predation stress and the
679 nutritional ecology of a generalist herbivore. Ecology 97:3119-3130

680 Sentis A, Hemptinne JL, Brodeur J (2014) Towards a mechanistic understanding of temperature
681 and enrichment effects on species interaction strength, omnivory and food-web structure.
682 Ecology letters 17:785-793

683 Sperfeld E, Wagner ND, Halvorson HM, Malishev M, Raubenheimer D (2017) Bridging ecological
684 stoichiometry and nutritional geometry with homeostasis concepts and integrative models
685 of organism nutrition. Functional Ecology 31:286-296

686 Steen H, Moy FE, Bodvin T, Husa V (2016) Regrowth after kelp harvesting in Nord-Trøndelag,
687 Norway. ICES Journal of Marine Science: Journal du Conseil 73:2708-2720

688 Steneck R, Watling L (1982) Feeding capabilities and limitations of herbivorous molluscs: a
689 functional group approach. Marine Biology 68:299-319

690 Teagle H, Smale DA (2018) Climate-driven substitution of habitat-forming species leads to
691 reduced biodiversity within a temperate marine community. Diversity and Distributions
692 24:1367-1380

693 Tyberghein L, Verbruggen H, Pauly K, Troupin C, Mineur F, De Clerck O (2012) Bio-ORACLE:
694 a global environmental dataset for marine species distribution modelling. *Global ecology*
695 *and biogeography* 21:272-281

696 Tyler P, Young CM, Serafy K (1995) Distribution, diet and reproduction in the genus *Echinus*:
697 evidence for recent diversification? In: Emson RH, Smith AB, Campbell AC (eds)
698 *Echinoderm Research 1995*. Balkema, Rotterdam, pp 29-38

699 Underwood AJ (1997) *Experiments in ecology: their logical design and interpretation using*
700 *analysis of variance*. Cambridge University Press, Cambridge, UK

701 Vanderklift MA, Kendrick GA, Smit AJ (2006) Differences in trophic position among sympatric
702 sea urchin species. *Estuarine, Coastal and Shelf Science* 66:291-297

703 Vergés A, McCosker E, Mayer-Pinto M, Coleman MA, Wernberg T, Ainsworth T, Steinberg PD
704 (2019) Tropicalisation of temperate reefs: implications for ecosystem functions and
705 management actions. *Functional Ecology* 33:1000-1013

706 Wernberg T, Krumhansl KA, Filbee-Dexter K, Pedersen MF (2019) Status and trends for the
707 world's kelp forests. In: Charles S (ed) *World Seas: An Environmental Evaluation*, vol
708 *Volume III: Ecological Issues and Environmental Impacts*, 2nd Edition edn. Elsevier., pp
709 57-78

710 Wernberg T, Thomsen MS, Tuya F, Kendrick GA, Staehr PA, Toohey BD (2010) Decreasing
711 resilience of kelp beds along a latitudinal temperature gradient: potential implications for a
712 warmer future. *Ecology Letters* 13:685-694

713 Whalen MA, Whippo RDB, Stachowicz JJ, York PH, Aiello E, Alcoverro T, Altieri AH, Benedetti-
714 Cecchi L, Bertolini C, Bresch M, Bulleri F, Carnell PE, Cimon S, Connolly RM, Cusson
715 M, Diskin MS, D'Souza E, Flores AAV, Fodrie FJ, Galloway AWE, Gaskins LC, Graham
716 OJ, Hanley TC, Henderson CJ, Hereu CM, Hessing-Lewis M, Hovel KA, Hughes BB,
717 Hughes AR, Hultgren KM, Jänes H, Janiak DS, Johnston LN, Jorgensen P, Kelaher BP,
718 Kruschel C, Lanham BS, Lee K-S, Lefcheck JS, Lozano-Álvarez E, Macreadie PI, Monteith
719 ZL, O'Connor NE, Olds AD, O'Leary JK, Patrick CJ, Pino O, Poore AGB, Rasheed MA,
720 Raymond WW, Reiss K, Rhoades OK, Robinson MT, Ross PG, Rossi F, Schlacher TA,
721 Seemann J, Silliman BR, Smee DL, Thiel M, Unsworth RKF, van Tussenbroek BI, Vergés
722 A, Yeager ME, Yednock BK, Ziegler SL, Duffy JE (in press) Climate drives the geography
723 of marine consumption by changing predator communities. *Proceedings of the National*
724 *Academy of Sciences of the United States of America*
725

726 **Table & figure captions**

727

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

Response variable	Transf	Disp	PERMANOVA Factor			%var Re, Si, Res
			<i>F</i> Region (Re)	<i>F</i> Site (Si)	<i>df</i> Re, Si, Res	
Seaweed biomass (kg m⁻²)						
<i>Laminaria hyperborea</i>	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						
<i>Laminaria hyperborea adults</i>	SQRT	ns	21.75*	3.32*	3, 4, 40	80, 05, 15
<i>Laminaria hyperborea young</i>	LOG	m	22.39**	2.26ns	3, 4, 40	77, 04, 19
<i>E. esculentus</i>	none	***	90.38*	0.48ns	3, 4, 122	78, 00, 22
d15N						
<i>Laminaria hyperborea adults</i>	none	ns	56.36***	0.79ns	3, 4, 40	78, 00, 22
<i>Laminaria hyperborea young</i>	none	***	1.68ns	18.26***	3, 4, 40	21, 59, 20
<i>E. esculentus</i>	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)

734
735 **Figure 1.** Mean biomass (kg m⁻²) of kelp (A, B) and other seaweed categories (C, D) across study
736 sites. Around the median (horizontal line), the box plots show the quartiles, the 95% confidence
737 intervals (whiskers) and the outliers. Letters, superscript stars (*) indicate pair-wise differences (P
738 < 0.05) among regions and among sites within regions, respectively. Note that the scale differs
739 among panels.

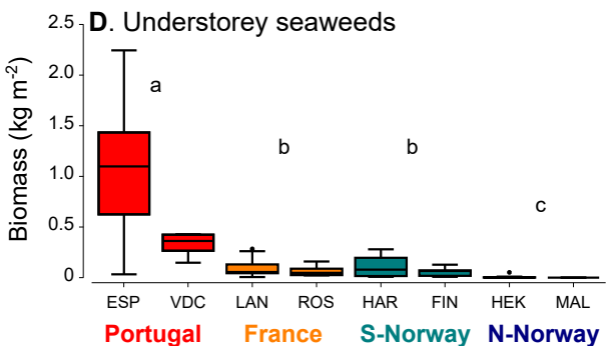
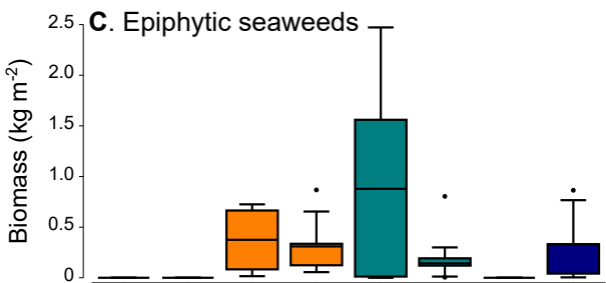
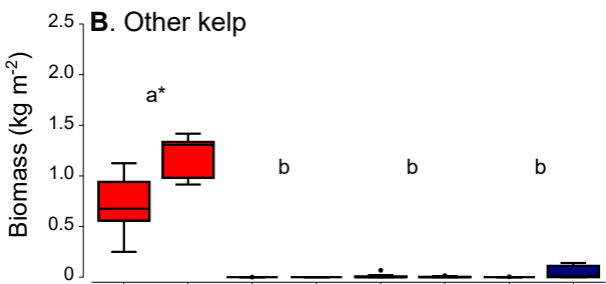
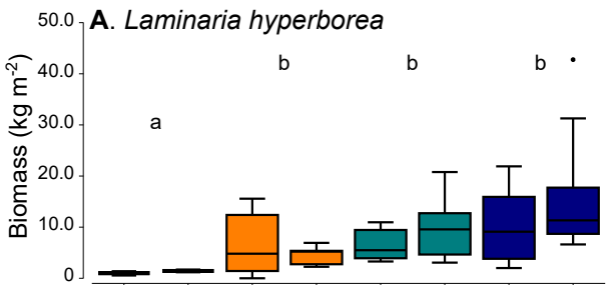
740
741 **Figure 2.** Fleshy seaweed (kelp and crustose algae excluded) and sessile fauna percentage cover
742 (%) estimated upon stipe (epiphytes) and bedrock habitats (understory). The box plots show the
743 total covers (with Q1, Median, Q3, 95% C.I.s and outliers). The heat maps illustrate the covers of
744 the dominant morpho-functional groups (average SIMPER contribution > 5%) of fleshy seaweeds,
745 sessile fauna and others. For each category, letters indicate differences among regions, within
746 which superscript stars indicate differences among sites according to PERMANOVA pairwise
747 tests.

748
749 **Figure 3.** Trophic level (A), contribution of the main food items (B, average SIMPER contribution
750 > 5%) to the diet composition (C) of *Echinus* within and across study sites. Around the median
751 (horizontal line), the box plots show the quartiles, the 95% confidence intervals (whiskers) and the
752 outlier. Letters and superscript stars indicate pair-wise differences among regions and among sites,
753 respectively.

754

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

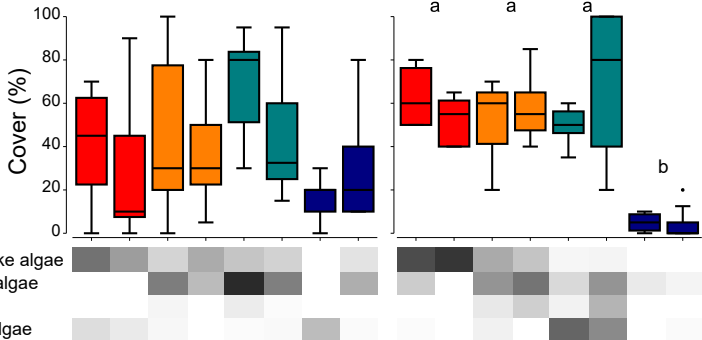
760



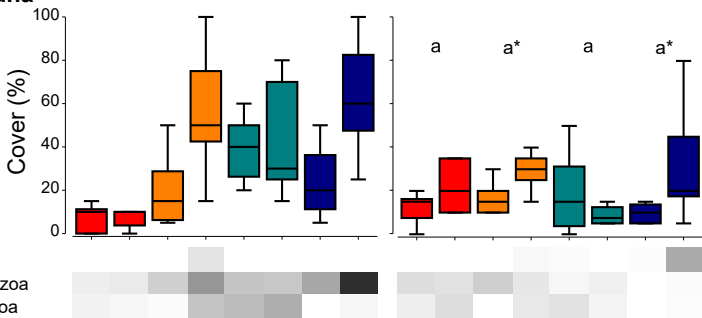
Epiphytes

Understorey

Fleshy seaweed

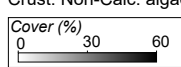


Sessile fauna

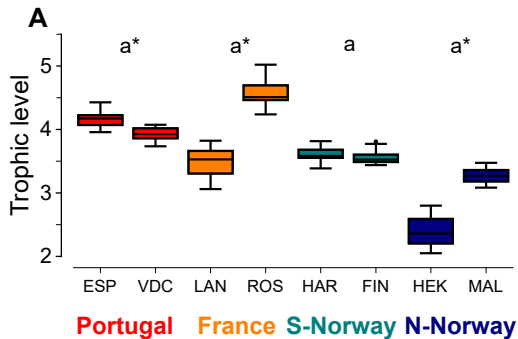


Others

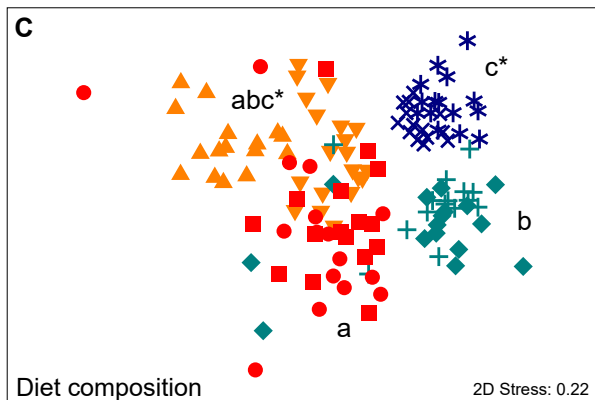
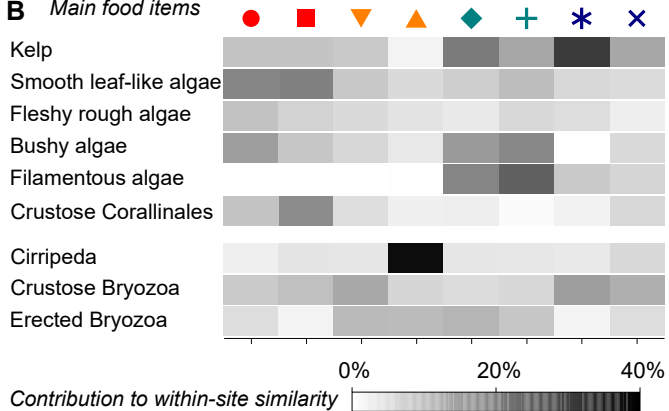
Sand
Crust. Calc. algae
Crust. Non-Calc. algae

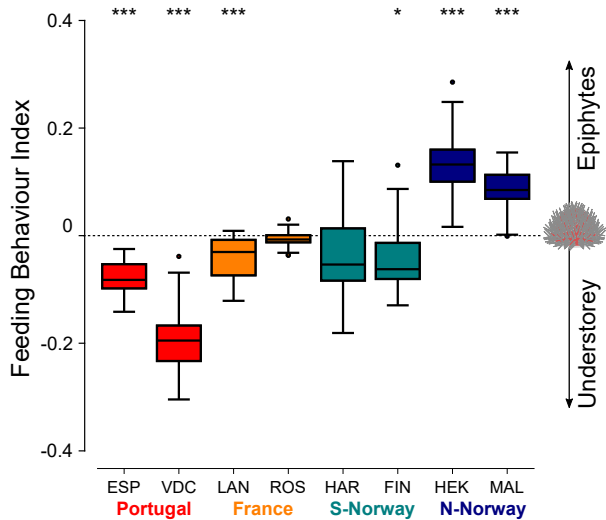


ESP VDC LAN ROS HAR FIN HEK MAL
Por **Fra** **S-Nor** **N-Nor**
Por **Fra** **S-Nor** **N-Nor**



B Main food items



A**B**