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

Leclerc, JeanCharles; de Bettignies, Thibaut ; de Bettignies, Florian ; Christie, Hartvig ; Franco, João N. ; Leroux, Cédric ; Davoult, Dominique ; Pedersen, Morten Foldager; FilbeeDexter, Karen ; Wernberg, Thomas

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Jean-Charles Leclerc[1,2*], Thibaut de Bettignies[3,4], Florian de Bettignies[1], Hartvig Christie[5], João N Franco[6,7], Cédric Leroux[8], Dominique Davoult[1], Morten F. Pedersen[9], Karen Filbee-Dexter[4,10], Thomas Wernberg[4,9,10]

[1]Sorbonne Université, CNRS, UMR 7144 AD2M, Station Biologique de Roscoff, Place Georges Teissier, 29680 Roscoff, France

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

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

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

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

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

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

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

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

[10]Benthic Communities Research Group, Institute of Marine Research, His, Norway

*leclercjc@gmail.com

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.

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

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 biennnis* 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 theorotical 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

METHODS

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 m^2 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 × 100

194   × 8 mm), where the bottom was divided into 200 square compartments (5 × 5 × 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 $\delta^{15}N$ 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 × 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 $\delta^{15}N$ 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): $\delta^{15}N = [(^{15}N/^{14}N_{sample} / {}^{15}N/^{14}N_{reference}) - 1] \times 10^3$. 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 $\delta^{15}N$ 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 (TL_{urchin}): $TL_{urchin} = 1$

229    $+ (\delta^{15}N_{urchin} - \delta^{15}N_{baseline}) / DDDF$, where $\delta^{15}N_{baseline}$ corresponds to the mean $\delta^{15}N$ of kelp

230   (averaged over adult and young kelps per site) and DDDF corresponds to diet-dependent

231   discrimination factor (Δ^{15}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 δ^{15}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 δ^{15}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 δ^{15}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 ± 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 ±

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 ± 4.5 kg$_{ww}$ m^{-2}, mean ± SD) to northern Norway (13.7 ± 11.3 kg$_{ww}$ m^{-2}, Fig. 1A, Table

303 1), where similar values were observed, but its biomass was much lower (< 0.1 kg$_{ww}$ m^{-2}) in

304 Portugal, where the canopy was dominated by the pseudo-annual kelp *Sacchoriza polyschides* (0.9

305 ± 0.3 kg$_{ww}$ 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 understorey biomass

309 (Fig. 1D). In northern Norway, the fleshy algal understorey was patchy, monospecific

310 (*Desmarestia aculeata* and the biomass was negligible (5.1 ± 15.6 g$_{ww}$ m^{-2}) when compared to

311 other regions (Table 1, Fig. 1D). Understorey biomass was similar in France (80.4 ± 78.1 g$_{ww}$ m^{-2})

312 and southern Norway (84.6 ± 831 g$_{ww}$ m^{-2}) and about ten-fold lower than in Portugal (775.9 ± 665.5

313 g$_{ww}$ 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 understorey 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 (δ^{15}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 δ^{15}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 understorey (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 understorey 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 understorey, 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 understorey 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 understorey 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 understorey 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 understorey,

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 understorey 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

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.

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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)

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