Stable-isotope based location in a shelf sea setting: accuracy and precision are comparable to light-based location methods.

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1. Retrospective determination of location for marine animals would facilitate investigations of migration, connectivity and food provenance. Predictable spatial variations in carbon and nitrogen isotopes in primary production across shelf seas provide a basis for stable isotope-based location.

2. Here we assess the accuracy and precision that can be obtained through dietary-isotope based location methods. We build isoscapes from jellyfish tissues and use these to assign scallops of fixed and known individual location, and herring with well-understood population-level distributions in the North Sea.

3. Accuracy and precision for retrospective isotope-based location in the North Sea was of a similar order to light-based location devices, with 75% of individual scallops assigned correctly to areas representing c.30% of the North Sea, with a mean linear error on the order of 10^2km. Applying assignment methods to an alternative migratory species (herring) resulted in ecologically realistic assignments consistent with fisheries survey data.

4. Location methods based on dietary isotopes such as carbon and nitrogen recover the spatial origin of nutrients assimilated into tissues and this may not correspond directly to the physical location if either the test animal or its prey is highly migratory. Stable isotope based location can be applied to any marine-feeding organism or derived food product, but the ecological meaning of any assigned area will be more difficult to interpret for large, high trophic level, migratory animals with relatively slow isotopic assimilation rates.

Key-words: Isoscape, assignment, provenance, connectivity, migration, spatial, marine, geolocation

43

44 **Introduction**

45 Understanding animal movements is fundamental to population dynamics,
46 predator-prey relationships, nutrient and energy fluxes within food webs and
47 management of human-animal interactions. In comparison to terrestrial animals,
48 marine (and aerial) animals encounter relatively few static, physical barriers to
49 movement and dispersal over areas large in comparison to body sizes is a
50 common phenomenon. In the context of marine fisheries, mislabelling of fishery
51 products has emerged as a major problem on global markets (Marko *et al.* 2004;
52 Wong and Hanner, 2008; Nielsen *et al*. 2012, Cawthorn *et al.* 2012). Tracing
53 marine food from origin to sale is a key aim of regulatory organisations
54 worldwide. At present there are few effective retrospective analytical methods
55 available to test claims of spatial origin of traded seafood.

56 Marine spatial ecology is undergoing a revolution with rapid
57 developments in telemetry and electronic tagging technology with the
58 deployment of large static acoustic arrays, satellite geo-location and the
59 development of ever smaller less invasive data storage tags (Hunter *et al.* 2003;
60 Righton *et al.* 2007; Block *et al.* 2011). Nonetheless, direct tagging of marine
61 animals still requires capture and recovery of tags, and processing of data, and is
62 relatively costly (Ramos & Gonzalez-Solis 2012). Furthermore, while tagging
63 experiments reveal individual movements in high resolution, by definition, they
64 cannot be applied retrospectively. Natural tags provide an attractive supplement
65 to direct location tools. Natural location methods typically attempt to link the
66 chemical (or parasite) composition of the test animal's tissues to known spatial
67 variations in the environment (Hobson 1999, Graham *et al.* 2010, Seminoff *et al.*

2012, McMahon *et al.* 2013). In recent years, stable isotope location has proven effective at reconstructing long-distance migrations in terrestrial, particularly avian, ecology (Rubenstein & Hobson 2004; Wunder and Norris 2008; Hobson *et al.* 2012). Statistical models of spatial variation in the isotopic composition of precipitation (Bowen, 2010), vegetation (West *et al.* 2007; Still & Powell 2010,) and higher taxa tissue (Vander Zanden *et al.* 2015) have been developed in many environments and termed isoscapes. Such isoscapes can provide a base model to assign geographic origin to a tissue of interest, following calibration between the media used to construct the isoscape and the species and tissue to be assigned (Wunder & Norris 2008). A relatively mature literature has developed describing the construction of isoscapes, the statistical considerations surrounding geographic assignment based on isoscapes, and application of isoscapes to track animal movements (West *et al.* 2010).

Isotope-based location comprises a geo-statistical spatial model, a calibration between the model and the species and tissue to be assigned, and a probabilistic comparison between model and measured data. Isoscapes derived from the same species and tissues as those that will be assigned in theory provide the most robust method of assignment. However, the practical and financial limitations associated with sampling and analysing tissues of each migratory species across the full potential foraging range are considerable. Therefore the potential for isotope-based geo-location is greatly increased if multiple taxa can be referred to a single isoscape model. The accuracy and precision available for isotope-based location therefore depends on the variance associated with the underlying geostatistical isoscape model, *in situ* variability in the isotopic compositions of both the organism used to construct the model and

93 in the tissues to be assigned, and the uncertainty inherent in linking the isotopic
94 compositions of the tissues to be assigned to the baseline isoscape (i.e.
95 calibration of the isoscape to the tissue of interest, Wunder & Norris 2008).
96 Considerable debate remains around the most effective way to incorporate error
97 and uncertainty into stable isotope-based geographic assignment methods
98 (Wunder & Norris, 2008; Van Wilgenburg *et al.* 2011; Wunder 2012; Bowen *et*
99 *al.* 2014, Vander Zanden *et al.* 2015). Wunder (2008) provides a thorough review
100 of the assumptions inherent in isotope-based location, focussing on hydrogen
101 and oxygen isotope based geo-assignment specifically in migratory birds.
102
103 Isotope-based location is not as well developed in marine settings and
104 very few robust assessments of the accuracy and precision obtained using
105 isotope based location have been developed in marine settings (Vander Zanden
106 *et al.* 2015). In marine systems oxygen and hydrogen isotopes are relatively
107 spatially constant, so alternative isotope systems are needed to provide spatial
108 information (Trueman *et al.* 2012). The isotopic composition of carbon and
109 nitrogen in marine primary production is predictably heterogenous over spatial
110 scales ranging from tens to thousands of kilometres (Jennings and Warr, 2003;
111 Somes *et al.* 2010; McMahon *et al.* 2013; Radabaugh *et al.* 2013, Jennings & van
112 der Molen 2015), and is passed through the food chain. Assigning location based
113 on carbon and nitrogen isotopic compositions therefore effectively tracks the
114 spatial origin of primary production fuelling higher trophic level production
115 rather than the direct spatial location of the animal tested. Nonetheless carbon
116 and nitrogen isotopes have been used extensively to track animal movements

117 across marine isotopic gradients (Hobsen & Schell, 1998; Jaegar *et al.* 2010,
118 MacKenzie *et al.* 2012).
119 Marine carbon and nitrogen isoscape models are generated by
120 interpolation from spatially explicit samples (Schell *et al.* 1998; McMahon *et al.*
121 2013). Sessile invertebrates such as filter feeding bivalves have often been used
122 to produce spatial isotope models (e.g. Jennings & Warr, 2003). However, the
123 distribution of sessile invertebrates is limited by water depth and substrate type
124 resulting in systematic variance in spatial coverage of reference samples across
125 the study region. Environmental correlates such as water temperature, depth
126 and salinity have been used to predict isotopic compositions in areas with no
127 reference samples (Jennings & Warr 2003; Barnes *et al.* 2009; MacKenzie *et al.*
128 2014), but the resulting isoscape models are strongly dependent on the location
129 of the reference samples and the assumption that regression relationships
130 between environmental drivers and isotope values derived in the sampled
131 region are constant throughout the wider study area. The uncertainty associated
132 with any predicted isotope value increases with (a) the error associated with the
133 regression model, (b) the spatial distance from the reference sites and (c)
134 isotopic or environmental differences between conditions at the predicted site
135 and the mean of the combined reference sites. Estimating the spatially varying
136 uncertainty associated with regression-based isoscape models is not trivial
137 (Bowen & Ravenaugh 2003), and has not been attempted for marine isoscapes.
138 An alternative approach lies in selecting pelagic reference organisms that are
139 widely distributed, but may have larger between-individual variance associated
140 with movement or diet ecology. Scyphomedusan jellyfish provide an attractive
141 potential target due to their ubiquitous distributions, rapid growth and short

142 lifespans (MacKenzie et al 2014). While scyphomedusan jellyfish are mobile,
143 movement is relatively passive and isotopic assimilation rates are fast. The
144 isotopic half-life for the moon jellyfish *Aurelia aurita,* for example, is estimated at
145 c.10 days (D'Ambra et al. 2014). The distance travelled by jellyfish during the
146 window of isotopic assimilation is therefore likely to be short compared to the
147 spatial scales of isotopic variance in open waters. Jellyfish may be a poor choice
148 for spatial isotope modelling in coastal areas where isotopic variability occurs at
149 smaller spatial scales.
150 Here we assess the precision and accuracy associated with using spatial
151 gradients in carbon and nitrogen isotopes to assign origin to animal tissues
152 across a relatively large shelf sea area. We derive carbon and nitrogen isoscapes
153 from lion's mane jellyfish *Cyanea capillata* expanding on the dataset and
154 methods outlined in (MacKenzie *et al.* 2014, Fig. 1). The North Sea is a shallow
155 semi-restricted shelf sea in the North Atlantic ocean with a total area of around
156 650,000km^2, sustaining one of the productive fisheries in the world. The North
157 Sea comprises a seasonally-stratified northern basin with a mean depth >50m,
158 and a shallower southern basin that is not stratified. In this study we quantify
159 the accuracy and precision associated with isotope-based geo-location in the
160 North Sea using two independently-determined datasets of stable isotope
161 compositions of the sessile queen scallop *Aequipecten opercularis* (Jennings *et al.*
162 2002, Jennings & van der Molen, 2015). We then identify feeding locations of 351
163 herring *Clupea harengus* caught at known locations throughout the North Sea.
164

165 ## Materials and methods

166

STABLE ISOTOPE SAMPLES

Following methods described in MacKenzie *et al.* (2014), 66 individuals of *C. capillata* were sampled from 52 stations in the North Sea in August 2015 during the International Bottom Trawl Survey on board the RV Cefas Endeavor. Jellyfish were collected, weighed and measured, and a section of bell tissue (mesoglea) removed and immediately frozen. Jellyfish ranged in size from 80 to 240mm in diameter (mean = 107mm, σ = 3.25mm). In the laboratory, tissues were washed 3 times with water to remove any soluble nitrogenous materials, re-frozen prior to freeze-drying, sub-sampling and submission for isotopic analyses. Capture locations, body sizes and isotope data for jellyfish tissues are reported in Table S1 and locations are illustrated in Fig. 1.

351 individual herring were captured at 41 known locations within the North Sea during September 2011 as part of the International Bottom Trawling Survey. Fishing was conducted from the R.V. “Cefas Endeavor”. After capture, herring were weighed, dorsal muscle was excised and frozen prior to analysis. Herring under 200mm standard length were grouped as ‘small’ fish, likely to represent juveniles, whereas fish greater than 200mm standard length are likely to be mature (ICES, 2012). Muscle samples were freeze dried, ground to a powder and analysed for carbon and nitrogen isotopic composition. Capture locations, body sizes and isotope data for herring muscle are reported in Table S2 and locations are illustrated in Fig. 2.

191 Analyses were performed by either OEA laboratories or Elemtex laboratories,
192 Cornwall, UK. Accuracy and precision were monitored through laboratory
193 internal standards (USGS 40 and USGS 41 and a bovine liver standard) and
194 repeat blind analyses of an in-house comparison standard (ARCOS glutamic acid)
195 nested within samples. Accuracy in both laboratories for $\delta^{13}C$ and $\delta^{15}N$ values
196 was within 0.1‰ of long-term average values for this standard, and precision
197 was 0.2‰ for $\delta^{13}C$ and 0.17‰ $\delta^{15}N$ values.
198 Jellyfish bell tissue $\delta^{13}C$ values showed a significant negative linear
199 relationship with C:N ratios (p = 4.54e-05, slope = -0.047, Adjusted R^2 = 0.2),
200 implying a variance component related to the concentration of isotopically light
201 lipids within the sample. To correct for potential lipid-related variance in $\delta^{13}C$
202 values, measured $\delta^{13}C$ values were adjusted to those predicted for a lipid-free
203 protein (atomic C:N ratio of 3.4) using linear regression between $\delta^{13}C$ values and
204 C:N ratios. We did not apply alternative arithmetic lipid correction terms as the
205 measured C:N ratios are close to those expected from pure protein with a small
206 range (mean = 3.6, σ = 0.15) implying that linear corrections are equally
207 effective (Kiljunen *et al.* 2006), and we therefore prefer to use correction terms
208 derived from the species and individuals studied. Lipid-corrected $\delta^{13}C$ values of
209 jellyfish show a positive correlation with bell diameter, accordingly they were
210 normalised to the median diameter (107mm):
211
212 $\delta^{13}C_{s.cor} = \delta^{13}C_{cor}+(\text{Diameter}-10.73)*0.19$ eqn 1
213

214 Herring muscle contained varying C:N ratios, and $\delta^{13}C$ values were corrected for
215 lipid content arithmetically (Kiljunen et al. 2006).
216
217 Isotopic data from queen scallops was recovered from Jennings & Warr
218 (2003) and Barnes *et al.* (2009) for scallops sampled between 25 July and 29
219 September 2001, and from S. Jennings (*pers. comm.* 2016) for scallops sampled in
220 similar locations in the summer of 2010 (Jennings & van der Molen, 2015). Up to
221 seven individual scallops were sampled in each area. Locations of capture sites
222 are shown in Fig. 2, Details of sampling, preparation and analytical
223 methodologies are provided in Jennings & Warr (2003), Barnes *et al.* (2009) and
224 Jennings & van der Molen, 2015.
225
226 STATISTICAL ASSIGNMENT METHODS
227
228 Statistical models of spatial variation in the isotopic composition of carbon and
229 nitrogen in jellyfish tissues sampled in 2015 were drawn from the lipid and size-
230 corrected isotope data using Linear Kriging. Isoscapes are presented in Fig. 1
231 together with the associated spatial variances, and locations of jellyfish sampled
232 to create the isoscapes. Raster files of the isoscape values are provided as
233 supplementary data.
234
235 In isotope-based Geo-assignment, the likelihood or probability of the sample
236 originating from a given location or cell in the isoscape depends on the isotopic
237 difference between the sample and cell value relative to the total variance in the
238 isoscape. As described above, much of the difficulty associated with isotope-

239 based location lies in quantifying sources of variance, a problem that is
240 particularly acute when using environmental correlates to extend predictions
241 into regions with no reference samples.
242 As our isoscape model does not contain values predicted from regression
243 models, variance associated with the isoscape is composed of a spatially varying
244 term related only to the physical distance between sample points estimated from
245 the kriging process, and a fixed term reflecting measurement error and between-
246 individual variance (Bowen *et al.* 2014). Measurement error associated with
247 jellyfish analyses determined as the standard deviation from 13 replicate
248 analyses of the glutamic acid standard was 0.2‰ for $\delta^{15}N$ and 0.1‰ for $\delta^{13}C$
249 analyses. Between-individual variances in jellyfish isotope compositions were
250 estimated from jellyfish sampled both in 2011 (MacKenzie *et al*. 2014) and in
251 2015 as 1.69‰ and 1.04‰ for $\delta^{13}C_{cor}$ and $\delta^{15}N$ values respectively. These
252 between-individual variance estimates are similar to those provided for
253 gelatinous zooplankton by Nagata *et al*., (2015) and Fleming *et al.,* (2015),
254 particularly when accounting for the marked effect of size on isotopic variance in
255 the Fleming *et al.* (2015) data. Total uncertainty in the assignment isoscape was
256 given by:
257
258 $$\sigma^2_{iso\ (x,y)} = \sigma^2_{k.iso\ (x,y)} + \sigma^2_{m.iso\ (x,y)} + \sigma^2_{bi.iso\ (x,y)} \quad \text{eqn 2}$$
259
260 where $\sigma^2_{iso\ (x,y)}$ is the pooled variance associated with the isoscape prediction,
261 $\sigma^2_{k.iso\ (x,y)}$ is the variance associated with the spatial interpolation model, $\sigma^2_{m.iso}$

$_{(x,y)}$ is the variance associated with measurement error and $\sigma^2_{bi.iso\ (x,y)}$ is the variance associated with *in situ* between-individual variation.

Measurement error associated with $\delta^{15}N$ analyses of scallop tissues was <0.2‰, and the mean standard deviation between individual scallops was 0.8‰, similar to between-individual variance in *C. capillata* $\delta^{15}N$ values (Jennings & Warr 2003, Jennings & van der Molen 2015). We estimate associated measurement precision associated with $\delta^{13}C$ values in scallop tissues as 0.2‰, similar to measurement errors associated with $\delta^{13}C$ analyses of *C capillata*. Between-individual variance in lipid-corrected $\delta^{13}C$ values of scallops across 22 stations sampled in 2010 was 0.21‰ (Jennings *pers. comm.* 2016).

Pooled error associated with the measurement of scallop stable isotope compositions is therefore given by:

$$\sigma^2_{assign\ (x,y)} = \sigma^2_{m.assign\ (x,y)} + \sigma^2_{bi.assgn\ (x,y)} \qquad \text{eqn 3}$$

where $\sigma^2_{assign\ (x,y)}$ is the pooled variance associated with the isoscape prediction, $\sigma^2_{m.assign\ (x,y)}$ is the variance associated with measurement error and $\sigma^2_{bi.assign\ (x,y)}$ is the variance associated with *in situ* between individual variation.

Uncertainties associated with calibration between the isoscape model and the tissue to be assigned were estimated from the combined uncertainty associated with trophic separation and trophic fractionation between jellyfish and scallops (e.g Wunder & Norris 2008). Trophic separation between jellyfish and scallops was constrained from known diet preferences. Scallops are filter-feeding molluscs sustained primarily on detrital phytoplankton and

microzooplankton. Lion's mane jellyfish are opportunistic pelagic predators consuming a range of macro-zooplankton and larval/juvenile fish. The jellyfish sampled in 2015 encompassed a relatively narrow size range from 80 to 240mm bell diameter equivalent to a wet mass of c. 100-500g, and no systematic size-related difference in trophic level between sampled individuals is expected (Fleming *et al.,* 2015). Mass balance (Ecopath) modelling of the North Sea community (Mackinson & Daskalov, 2007) estimates scallop and gelatinous zooplankton trophic levels as 2.8 and 3.6 respectively. We therefore estimate the trophic distance between *C. capillata* and *A. opercularis*, as a single trophic level and assign uncertainty to that estimate with standard deviation of 0.25, ensuring that 95% of the estimates of trophic distance between scallops and *C. capillata* fall between 0.5 and 1.5 trophic levels.

Isotopic fractionation between tissue and diet (trophic fractionation) is estimated as 3.4‰ for nitrogen and 1‰ for carbon (Vander Zanden & Rasmussen, 2001) with a standard deviation of 0.5‰ ensuring that 95% of the estimates of isotopic trophic fractionation fall between 2.4 and 4.4‰ for nitrogen and between 0 and 2‰ for carbon. We then created 10,000 trophic fractionation and trophic distance values drawn from the distributions described above and estimated the distribution of isotopic separation values between jellyfish and scallops.

Scallop muscle and jellyfish bell tissue have contrasting biochemical compositions and therefore have potential for additional isotopic offsets. We do not know of any studies reporting isotopic discrimination between jellyfish bell tissue and coexisting muscle while accounting for trophic level. As all scallops are known to derive from the isoscape area, trophic-level corrected values

should lie within the total range of isotopic vales within the isoscape. We therefore compare trophic level-corrected scallop data to the full range of $\delta^{13}C$ and $\delta^{15}N$ values contained in the isoscape, and apply the smallest offset term required to ensure that all measured scallop values lie within the range described by the isoscape. For scallops we therefore apply an additional tissue-specific adjustment of +1‰ ($\sigma = 0.5$) for $\delta^{15}N$ and +0‰ ($\sigma = 0.5$) for $\delta^{13}C$ values. The final correction also accounts for any systematic under or over-estimation of trophic differences or isotopic fractionation. The estimated variance associated with calibration between scallop and jellyfish tissues σ^2_{calib} is therefore composed of the variance in estimated isotopic spacing across the 10,000 draws and the estimated variance around the remaining tissue calibration offset

$$\sigma^2_{calib(x,y)} = \sigma^2(TD*TF_{(x,y)}) + \sigma^2_{off\ (x,y)} \quad \text{eqn 4}$$

where x and y refer to $\delta^{13}C$ and $\delta^{15}N$ values respectively, TD is the distribution of trophic difference values, TF is the distribution of isotopic fractionation values and σ^2_{off} is the estimated variance associated with the tissue offset.

We apply the method outlined above to quantify variance terms associated with assigning herring to the same *C. capillata*-defined isoscape. Herring are gape-limited zooplankton feeders with a similar diet and trophic level to predatory jellyfish. Ecopath modelling assigns herring a trophic level of 3.4 and gelatinous zooplankton a trophic level of 3.6 (Mackinson & Daskalov 2007). We therefore assign a trophic difference between herring and *C. capillata* of -0.5 with a standard deviation of 0.5. Multiple individuals were sampled in all

41 locations, and mean between-individual standard deviations were 0.44‰ for $\delta^{15}N$ and 0.39‰ for lipid-corrected $\delta^{13}C$ values. Minimum tissue offset values between herring and jellyfish were estimated as described above as +2‰ (σ=0.5) for $\delta^{13}C$ and +0.5‰ (σ 0.5) for $\delta^{15}N$. A summary of assignment conditions is provided in Table 1.

We follow the assignment approach outlined in Vander Zanden et al. 2015:

$$f(x, y \mid \boldsymbol{\mu}_i, \boldsymbol{\Sigma}) = \frac{1}{\left(2\pi\sigma_x\sigma_y\sqrt{1-\rho^2}\right)} \times \exp\left(-\frac{1}{2(1-\rho^2)}\left[\frac{(x-\mu_x)^2}{\sigma_x^2} + \frac{(y-\mu_y)^2}{\sigma_y^2} + \frac{2\rho(x-\mu_x)(y-\mu_y)}{\sigma_x\sigma_y}\right]\right)$$

eqn 5

where $f(x,y|\mu_i,\Sigma)$ represents the probability that an individual with adjusted isotopic composition ($\delta^{13}C$=x and $\delta^{15}N$=y) originates from a given cell (i) within the isoscape with mean isotopic composition equal to the components of vector μ_i, and variance co-variance matrix Σ. ρ is the correlation between $\delta^{13}C$ and $\delta^{15}N$ values throughout the isoscape, σ_x and σ_y are the pooled standard deviations in $\delta^{13}C$ and $\delta^{15}N$ values respectively given by the sum of the variances:

$$\sigma_{(x,y)} = \sqrt{\left(\sigma^2_{iso\ (x,y)} + \sigma^2_{assign\ (x,y)} + \sigma^2_{off\ calib(x,y)}\right)}$$

eqn 6

353 The range in pooled error terms across the isoscape for scallop assignment was
354 3.5-12.4‰ for $\delta^{13}C$ values and 5.5-11.6‰ for $\delta^{15}N$ values, approximately three
355 times higher than the pooled error estimates provided by Vander Zanden *et al.*
356 (2015) where no calibration was needed between isoscape and assignment
357 tissue.
358
359 DISPLAYING ASSIGNMENT OUTCOMES
360
361 The outcome of stable-isotope based location can be displayed as continuous
362 surfaces, but it is easier to describe accuracy and precision based on discrete
363 assignments to a probable area defined by a probability threshold (i.e. an area
364 containing all sites with an assignment probability higher than an arbitrarily
365 fixed value). We use odds ratios to set threshold values (Van Wilgenburg *et al.*
366 2012, Vander Zanden *et al.* 2015). The odds of an event occurring is given by the
367 probability of the event occurring relative to the probability of that event not
368 occurring (or P/1-P). Thus a likely event has high odds. Here we define the odds
369 *ratio* as the ratio of odds of the outcome occurring compared to the odds of the
370 most likely outcome possible given the available data:
371
372 $$\text{Odds Ratio} = (P/1-P_i)/(P/1-P_{i.max}) \qquad \text{eqn 7}$$
373
374 By setting an odds ratio threshold, all cells with probability values greater than
375 the threshold are defined as cells of likely origin. The reciprocal of the odds ratio
376 gives the total proportion of data (and thus the total proportional area) expected
377 within the threshold limit according to the normal probability density function.

For instance, an odds ratio threshold of 2:1 includes all cells representing the most likely 2^{-1} = 50% of all data outcomes and defines a region of likely origin that is 50% of the total isoscape area. The precision of isotope-based assignment is thus defined by the odds ratio threshold, and the accuracy is given by the proportion of assigned individuals where the true location is contained within the assigned area (Vander Zanden *et al.* 2015).

Results

ISOSCAPES

The spatial isotope models (isoscapes) derived from *C. capillata* are shown in Fig. 1 A,B. Broad spatial patterns are similar to those shown in Jennings *et al.* 2003; Barnes *et al.* 2009; MacKenzie *et al.* 2014 and Jennings & van der Molen 2015, indicating consistent and temporally stable spatial isotopic gradients, and isotopic ranges that are conserved between pelagic and benthic feeding organisms. The newly derived isoscapes are drawn from samples with relatively regular spacing across the modelled area, and the variance associated with the new isoscape models is relatively low and constant across the region Fig 1 C,D.

ASSIGNMENT ACCURACY AND PRECISION

The accuracy associated with assigning a geographic origin to the two temporally distinct scallop tissue datasets considering uncertainties in calibration terms and between-individual variance is shown in Fig. 3. The assignment method provides better than random accuracy at all odds ratio

thresholds (Fig. 3). Assignments are >90% accurate when assigning to areas that on average represent >40% of the total area of the North Sea. Precision is enhanced at the expense of accuracy: Doubling the assignment precision to areas encompassing 20% of the total North Sea reduces accuracy to 50%. The mean linear error between the cell of maximum likelihood and the known location was 226 (σ = 137) km for the 2001 scallop data and 318 (σ = 114) km for the 2010 scallop data.

HERRING ASSIGNMENT

Herring were assigned to likely feeding areas using the assignment parameters outlined in Table 1. To report pooled results, individual herring areas were grouped according to body size. Following Van Wilgenburg *et al.* (2011), for each fish, cells designated as likely feeding areas were assigned a value of 1 and all other calls assigned a value of 0. Values were then summed for each cell across the total number of individual fish and divided by the total number of fish, providing an index of the most frequently assigned cells ranging between 0 and 1 (Fig. 4). Irrespective of capture location, larger fish are assigned to feeding areas in the central northern North Sea (Fig. 4A), consistent with summer fishery catches (ICES 2012, Fig. 4C). Smaller (juvenile) herring are assigned to feeding areas in the southern North Sea particularly around the German Bight (Fig. 4B), again consistent with locations of juvenile herring inferred from acoustic surveys (ICES 2012, Fig. 4D).

Discussion

ISOTOPE-BASED LOCATION ACCURACY AND PRECISION

Despite combined uncertainties associated with measurement, between individual variance, and calibration between an isoscape and measured tissues, isotope-based location was 75% accurate to 30% of the North Sea, equivalent to a spatial precision on the order of 10^5 $km^{2.}$ The mean linear error between the single cell of highest probability and the known location was between 200 and 300 km. Light-based location is widely used in animal ecology, but relatively few studies have tested accuracy of light based location. Where direct tests have been reported, mean errors of location by light range between around 200-400km (Phillips *et al.* 2004; Lisovski *et al.* 2012), approximately equivalent to linear errors reported here for isotope-based location methods.

The isoscape used here is derived from a mobile pelagic organism, but used to assign origin to a sessile benthic organism collected either 4 or 14 years prior to the samples used to derive the isoscape. This mismatch in sample collection time and organism functional group is deliberate, testing the degree to which isoscapes derived from a single reference organism can be used to assign a wide range of taxa over unspecified periods of time.

Short and long-term temporal variation in isotopic baselines could confound the use of isotopes for geolocation. Scallops have been sampled in 2001 and 2010, and jellyfish in 2011 (MacKenzie *et al.,* 2014) and 2015. The regional distribution of isotope values was consistent across these four independent sampling dates,

453 although the exact location of boundaries between isotopically distinct regions
454 varies slightly between sample suites. Consequently assignment accuracy is
455 relatively consistent between the two test datasets (Fig. 3). This is consistent
456 with broad hydrological control over spatial distribution of isotope values,
457 modified by relatively minor intra-year variability (MacKenzie *et al.,* 2014;
458 Jennings & van der Molen 2015). While jellyfish mesoglea sample spring and
459 summer production, scallops have a longer isotopic turnover times and likely
460 integrate annual average production (Jennings & van der Molen 2015). The
461 similarity between jellyfish and scallop isoscapes further supports the argument
462 that spring and summer primary production dominates biomass-weighted
463 consumer tissue production in this strongly seasonal sea. At higher spatial
464 resolution, or in coastal settings, isotopic compositions of primary production
465 and dissolved organic matter are expected to vary more widely in both time and
466 space (Kürten *et al.* 2013), and the spatial isotope models presented here are
467 unlikely to perform well.
468
469 GEOGRAPHIC ASSIGNMENT OF MIGRATORY FISHES
470
471 Herring present a particular challenge for fishery management, as they exhibit
472 complex migratory behaviour and variation in spawning strategies which change
473 in response to environmental conditions, population sizes, age structures and
474 harvesting (Dickey-Collas et al. 2010). North Sea herring feed in open waters in
475 the northern North Sea in summer months, before migrating south and east to
476 spawn in discrete locations dictated by the need for well-oxygenated coarse
477 substrates. Larval herring drift eastwards within the southern North Sea

towards the German Bight before recruiting to the adult population. Isotope-based geo-assignment captures this ontogenetic migration (Fig. 4), implying that isotope based location offers a promising additional tool for marine spatial ecology and management.

IMPLICATIONS FOR ECOLOGY, MANAGEMENT AND FOOD TRACEABILITY

Stable isotope-based retrospective location is well-established in terrestrial ecology, particularly for birds, but extension into marine environments has been slow due to the difficulty of obtaining baseline spatial isotope data. Here we show that isotopic baselines derived from carbon and nitrogen isotopic compositions of pelagic gelatinous zooplankton provide sufficient spatial resolution to rival light-based location in terms of accuracy and precision.

Determining location based on carbon and nitrogen isotope compositions records a fundamentally different ecological variable to other location methods. While data storage tag, satellite and water chemistry-based locations record the physical position of the animal, dietary isotope based locations record the likely spatial origin of nutrients assimilated during feeding. In sessile animals, or animals with a limited foraging range, feeding location and physical location will be effectively the same within the error of the assignment methods. In mobile animals (or animals feeding on mobile prey), however, assigned feeding location reflects the origin of primary production assimilated during feeding. Potentially, the location associated with assimilation of food may not necessarily correspond to the location where an animal spends the majority of its time.

Dietary isotope-based location provides additional ecological information beyond location at a fixed point in time, but interpreting the ecological meaning of dietary isotope 'location' in migratory animals requires some understanding of the timescale of isotopic assimilation relative to the rate and scale of movements across isotopic gradients. Herring are relatively small, metabolically-active, low trophic level (Mackinson & Daskalov 2007) fish, and isotopic equilibration is likely to occur with a half life on the order of c.50 days (Miller 2000; vander Zanden et al 2015). Consequently, isotopic-assignment areas for herring closely correspond to feeding areas. Dietary isotope-based identification of feeding grounds will be more problematic in animals where isotopic assimilation rates are slow with respect to movements across isotopic gradients. While static physical location tags (e.g. light or tidal-stream based location) can provide an answer to the question of where animals go (Hammerschlag *et al.* 2011), combinations of physical tags and isotopic location may go some way towards addressing questions of why animals spend time in particular regions.

The accuracy and precision of location methods based on carbon and nitrogen stable isotopes is highly dependent on the isotopic calibration between the baseline organism and the species and tissue to be assigned. Estimates of uncertainty associated with all steps in isotopic measurement, spatial modelling and calibration can be quantified and incorporated into assignment algorithms. Calibration methods and uncertainties must be reported with any stable isotope assignment. Nevertheless we suggest that stable isotope based geoassignment can be used in marine systems retrospectively to infer the location where the majority of nutrients were assimilated prior to capture. The method can in theory be applied to any marine feeding organism, but the ecological meaning of

any assigned area will be more difficult to interpret for high trophic level and migratory animals with relatively slow isotopic assimilation rates.

Acknowledgements

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Data accessibility

Jellyfish and herring isotope data and isoscape raster files are provided in the supplementary information. Stable isotope data from jellyfish, herring and previously published stable isotope data from Queen scallops sampled in 2001 are also available from (doi:10.5061/dryad.609hp). Stable isotope data from queen scallops sampled in 2010 are available from Cefas. The owner of the data, Simon Jennings, will be archiving it in Dryad shortly. The final version of this manuscript will include a direct link to this data. If you are viewing the 'Accepted Articles' version after September 2016, please search 'North Sea stable isotope' with Simon Jennings as the author in Dryad to find the relevant data.

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753 Supporting Information

754 Table S1. Locations of capture, bell diameter, bell weight and weight and stable
755 isotope composition ($\delta^{13}C$ and $\delta^{15}N$) for *C capillata* recovered across the North
756 Sea

757

758 Table S2. Locations of capture and stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$) for
759 *C harengus* recovered across the North Sea

760

761 C_raster.gri, C_raster.grd R-compatible raster files of the carbon isoscape model

762

763 N_raster.gri, N_raster.grd R-compatible raster files of the nitrogen isoscape
764 model

765

766 CVar_raster.gri, CVar_raster.grd R-compatible raster files of spatial variance in
767 the carbon isoscape model

768

769 NVar_raster.gri, NVar_raster.grd R-compatible raster files of spatial variance in
770 the nitrogen isoscape model

771

772

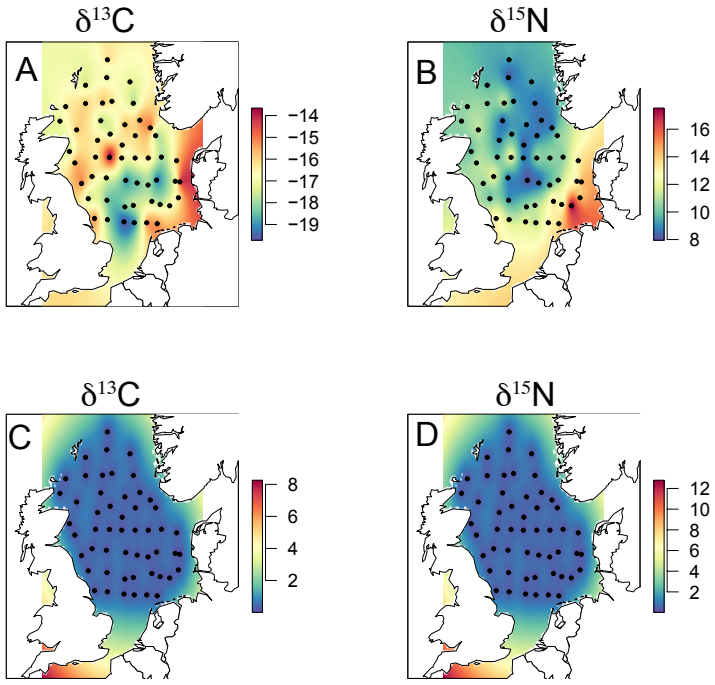
773 Table 1: Assignment conditions adopted for stable isotope based location of
774 scallops and herring against isoscapes derived from jellyfish tissues.

775

Variable	Isoscape jellyfish	Scallop calibration	Herring calibration
Measurement error	$\delta^{13}C$: 0.1, $\delta^{15}N$: 0.2:	$\delta^{13}C$: 0.2, $\delta^{15}N$: 0.2:	$\delta^{13}C$: 0.2, $\delta^{15}N$: 0.2:

(σ)	measured	estimated / measured	measured
Between-individual variance	$\delta^{13}C$: 1.69, $\delta^{15}N$: 1.04: measured	$\delta^{13}C$: 0.2, $\delta^{15}N$: 0.7: estimated / measured	$\delta^{13}C$: 0.2, $\delta^{15}N$: 0.2: measured
Trophic distance	NA	1 (σ = 0.25): literature estimate	-0.2 (σ = 0.25): literature estimate
Isotopic trophic fractionation	NA	$\delta^{13}C$: 1(σ = 0.5), $\delta^{15}N$: 3.4(σ = 0.5): literature compilation	$\delta^{13}C$: 1(σ = 0.5), $\delta^{15}N$: 3.4(σ = 0.5): literature compilation
Tissue specific fractionation	NA	$\delta^{13}C$: +0(σ = 0.25), $\delta^{15}N$: +1(σ = 0.25): graphical estimate	$\delta^{13}C$: +2(σ = 0.25), $\delta^{15}N$: +0.5(σ = 0.25): graphical estimate
Threshold odds ratio	NA	1.33	1.5

776



777

778 **Figure captions**

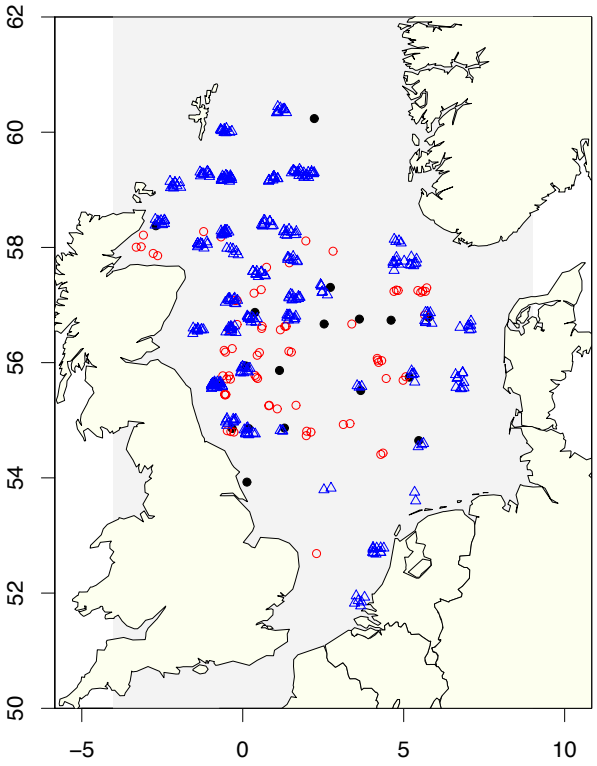
779

780

781 Fig. 1. Isoscape models (A, B) and associated variances (C,D) for $\delta^{13}C$ (A, C) and

782 $\delta^{15}N$ (B, D) values based on *C. capillata* sampled in September 2011. Sample

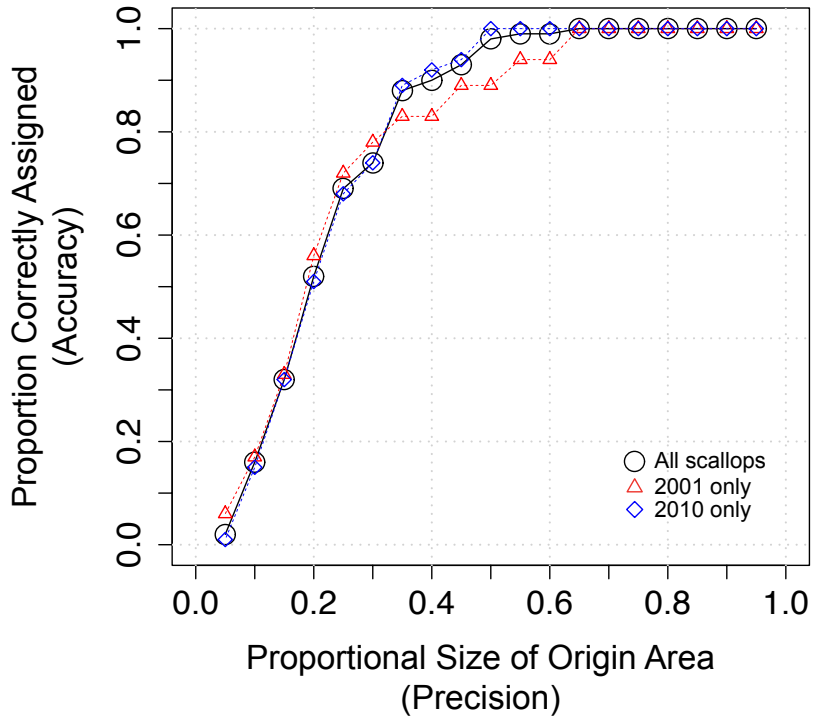
783 stations indicated with filled circles.



784

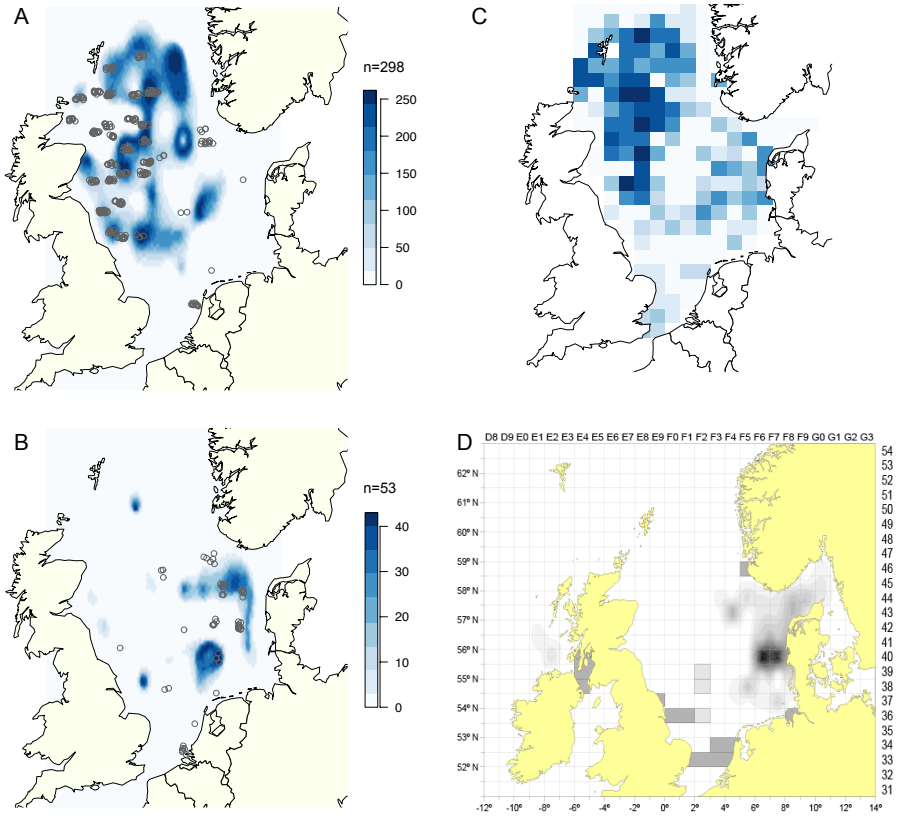
785 Fig. 2 Locations of herring (open triangles) and scallop (2001 data: filled circles,

786 2010 data: open circles) samples within the North Sea



787

788 Fig. 3 Accuracy and precision of assignment for the combined, 2001 and 2010
789 scallop datasets. Precision is defined by the probability threshold and expressed
790 as the proportion of data (i.e. cells) considered as likely. Accuracy is assessed as
791 the proportion of individual scallops where the threshold area contained the
792 known sample location.



793

794 Fig. 4. Comparison of isotope-based feeding area assignments and fisheries

795 survey data. A,B Most likely feeding areas for 351 North Sea herring sampled in

796 September 2011 as derived from stable isotope-based location. Colours

represent the number of individual herring assigned to each grid square. A) herring >200mm standard length, B herring <200mm standard length. Open circles indicate capture locations. C. Spatial distribution of reported landings of adult herring (log_{10} tonnes) in quarters 2 and 3 of 2011, data from (ICES 2012). D. Estimated biomass of immature herring in June-July 2011 from combined acoustic surveys (ICES 2012).