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Environmental correlates of large-scale spatial variation in the $\delta^{13}C$ of marine animals

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ABSTRACT

Carbon stable isotopes can be used to trace the sources of energy supporting food chains and to estimate the contribution of different sources to a consumer's diet. However, the $\delta^{13}C$ signature of a consumer is not sufficient to infer source without an appropriate isotopic baseline, because there is no way to determine if differences in consumer $\delta^{13}C$ reflect source changes or baseline variation. Describing isotopic baselines is a considerable challenge when applying stable isotope techniques at large spatial scales and/or to interconnected food chains in open marine environments. One approach is to use filter-feeding consumers to integrate the high frequency and small-scale variation in the isotopic signature of phytoplankton and provide a surrogate baseline, but it can be difficult to sample a single consumer species at large spatial scales owing to rarity and/or discontinuous distribution. Here, we use the isotopic signature of a widely distributed filter-feeder (the queen scallop *Aequipecten opercularis*) in the north-eastern Atlantic to develop a model linking base $\delta^{13}C$ to environmental variables. Remarkably, a single variable model based on bottom temperature has good predictive power and predicts scallop $\delta^{13}C$ with mean error of only 0.6‰ (3%). When the model was used to predict an isotopic baseline in parts of the overall study region where scallop were not consistently sampled, the model accounted for 76% and 79% of the large-scale spatial variability (10^1–10^4 km) of the $\delta^{13}C$ of two fish species (dab *Limanda limanda* and whiting *Merlangus merlangius*) and 44% of the $\delta^{13}C$ variability in a mixed fish community. The results show that source studies would be significantly biased if a single baseline were applied to food webs at larger scales. Further, when baseline $\delta^{13}C$ cannot be directly measured, a calculated baseline value can eliminate a large proportion of the unexplained variation in $\delta^{13}C$ at higher trophic levels.

1. Introduction

Stable isotope ratios are commonly used in ecological studies. From a food web perspective, carbon and nitrogen are the most important of the elements with naturally occurring stable isotopes, since they are abundant in plant and animal tissue. Typically, $\delta^{15}N$ and $\delta^{13}C$ values of a consumer are heavier than dietary inputs because the lighter isotopes are either preferentially excreted (^{14}N) or respired (^{12}C) (DeNiro and Epstein, 1978, 1981) and the extent of this enrichment is broadly predictable (DeNiro and Epstein, 1978; Minagawa and Wada, 1984; Post, 2002). However, for this knowledge to be useful when identifying food web sources and pathways, understanding of source materials is essential. Turnover times of primary producers such as phytoplankton and epiphytic algae are very high, so there may be variation in $\delta^{13}C$ and $\delta^{15}N$ on multiple time and space scales (Jennings et al., 1997; Vander Zanden and Rasmussen, 1999; Post, 2002). A temporally or spatially variable baseline could mask or distort interpretation of food web structure if these variations are not known and/or cannot be accounted for.

Plants with different modes of photosynthesis exhibit different carbon isotope values. $\delta^{13}C$ values can be used to differentiate between plants employing C3, C4 and CAM modes. C3 plants are greatly depleted in ^{13}C ($\delta^{13}C = -34$ to -22‰) whereas C4 and CAM plants generally have $\delta^{13}C$ values $= -20$ to -10‰. Although marine plants fix carbon using the C3 pathway they can have isotopic signatures that differ from those of terrestrial C3 plants (Gannes et al., 1998) and species and groups of marine primary producers may have distinctive signatures (e.g. Thomas and Cahoon, 1993; Jennings et al., 1997). Changes in base $\delta^{13}C$ ($\delta^{13}C_{base}$) are caused by differences in the $\delta^{13}C$ of utilized dissolved inorganic carbon (DIC) or by fractionation during DIC uptake and assimilation. There are, in general, three potential sources of DIC: respiration (re-mineralization) of organic carbon, atmospheric CO_2 and DIC from weathering of carbonates. The first is generally isotopically light (-20 to -35‰) (France, 2000) whereas atmospheric CO_2 and weathered carbonate are heavier (-7 and 0‰ respectively) (Post, 2002). In a given environment, $\delta^{13}C$ of marine primary producers is primarily controlled by the rate of dissolved CO_2 uptake (Laws et al., 1995) but related factors

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such as growth rate and taxon-specific differences and nutritional status can also be important (Burkhardt et al., 1999).

Carbon stable isotope ratios are often used to identify patterns of energy flow through food webs and the sources of energy that support them (DeNiro and Epstein, 1978; Tieszen et al., 1983; Post, 2002; Darnaude et al., 2004). In such applications, $\delta^{13}C$ data of consumers have to be linked to the $\delta^{13}C$ of source materials or animals that integrate some of the seasonal variation of primary producers. Filter-feeding bivalves have been used for this purpose for $\delta^{13}C$ in freshwaters (e.g. Vander Zanden and Rasmussen, 1999, 2001) and recent work has confirmed their suitability (Gustafson et al., 2007; Fukumori et al., 2008).

In small and contained environments, it is often straightforward to relate $\delta^{13}C_{base}$ to $\delta^{13}C$ in other parts of the food web, but this is not the case in open marine environments. First, larger animals at higher trophic levels are often very wide-ranging and have to be sampled at large spatial scales, but this may not be possible for source materials. Second, even if some consumers are known to integrate variation in $\delta^{13}C$ of primary producers, species and size related differences in consumer $\delta^{13}C$ are expected, and it is difficult to sample the same consumer species or size class at large spatial scales owing to local rarity and/or discontinuous distribution. Therefore, it is valuable to be able to predict $\delta^{13}C_{base}$ on a continuous basis over large spatial scales.

Here, we examine spatial variation in $\delta^{13}C_{base}$ of a bivalve mollusc that integrates local temporal variation in $\delta^{13}C$ and attempt to relate this spatial variation to physical properties of the environment. We use the resulting models to map $\delta^{13}C$ over large spatial scales and to account for observed variation in the $\delta^{13}C$ of two fish species and a fish community on scales of 10^1–$>10^4$ km.

2. Method

2.1. Sampling

Queen scallop *Aequipecten opercularis*, a widely distributed bivalve mollusc in European shelf seas, was used to determine $\delta^{13}C_{base}$. It is found on sand or gravel, sometimes at densities of several individuals per m^2, from the low tide mark to depths of around 100 m. It is a filter feeder, feeding on a combination of phytoplankton and associated bacterial and detrital material that supports benthic production (Graf et al., 1982; Billett et al., 1983). Two widely distributed fish species, dab (*Limanda limanda*) and whiting (*Merlangus merlangius*), plus bulk size-fractionated samples of fish from many sites, were used to assess $\delta^{13}C$ of animals and size-classes at higher trophic levels. Dab live mainly on sandy bottoms from 20 to 40 m, but up to 150 m (Wheeler, 1978). They feed mainly on cumaceans, amphipods, brittle stars and polychaetes (Knijn et al., 1993). Whiting are commonly found from 30 to 100 m, mainly on mud and gravel bottoms, but also on sand, rock and mid-water (Wheeler, 1978). They feed on benthic and pelagic food items including shrimps, euphausiids and fish (Daan, 1989; Hislop et al., 1997). The size-fractionated samples were used to provide an overall description of the food web, since body size explains most of the variation in trophic level in marine food webs.

Scallops, dab and whiting were caught with a Grande Ouverture Verticale (GOV) demersal trawl and 2 m or 4 m beam trawls. The 2 m beam trawl and GOV trawl were fished from R.V. "Cirolina" and the 4 m beam trawls from R.V. "Corystes". Stations in the North Sea, Celtic Sea and English Channel were fished using the standard protocol for fisheries surveys. The GOV and 4 m beam trawls were fitted with a cod-end of 20 mm stretched mesh and the 2 m beam trawl was fitted with a cod-end of 4 mm stretched mesh. The GOV and 4 m beam trawls were towed for 30 min at a speed of approximately 4 knots, while the 2 m beam trawl was towed for 5 min at 1 knot. All sampling was completed in the period 25 July 2001 to 29 September 2001. Further details of the sampling protocols are provided in Jennings and Warr (2003a).

At each site, up to 7 scallops were selected at random from all individuals with a shell height of 50–60 mm. They were weighed to 0.1 g and immediately frozen to −30 °C. On return to the laboratory, the scallops were partially thawed so a 1–2 g sample of adductor muscle tissue could be removed, refrozen, freeze-dried and ground to a fine powder (particles < 60 μm). Up to 3 dab and 3 whiting were also retained: dab were selected between 190 and 210 mm and whiting between 240 and 260 mm as fish isotopic signatures are known to increase with size even when fed on constant diet (Sweeting et al., 2007). Each fish was weighed to the nearest *g* and measured to the nearest mm. Approximately 2 g of white muscle was dissected from the dorsal musculature, placed in a vial and immediately frozen to −30 °C. At the laboratory the samples were freeze-dried and ground to a fine powder. To investigate complete fish communities, 74 sites in the North Sea were fished using an otter trawl net, towed for 30 min at 4 knots as described in Jennings and Warr (2003b). All fishes weighing more than 512 g were assigned to integer body-mass classes on a $\log_2$ scale; fishes weighing 512 g or less were randomly sub-sampled before being assigned. Samples of white muscle tissue, set at a fixed proportion of body weight, were dissected from 20 to 25 individuals in each class (or all fishes if <20). Tissue samples in each class were then combined and homogenized to produce a smooth paste. Approximately 4 g of this paste was retained, frozen to −30 °C and subsequently freeze-dried and ground.

2.2. Stable isotope analysis

Each sample of ground tissue was thoroughly mixed and a 1.0 mg sample weighed into a tin capsule for stable isotope analysis. The composition of the samples was determined using continuous flow isotope ratio mass spectrometry and ratios of ^{12}C:^{13}C are expressed in conventional delta notation (δ) relative to the international carbon standard Pee Dee Belemnite.

2.3. Environmental variables

At each site, the latitude, longitude and depth from which samples were collected were recorded. Mean surface and bottom temperatures are the mean annual temperatures over the previous 10 years, where annual temperatures were the mean of monthly temperature records in the relevant ICES (International Council for the Exploration of the Seas) rectangle (boxes of 0.5° North-South and 1° East–West; area of one rectangle 3720 km^2 at 53°N). Salinity was expressed as the mean surface salinity in the month of August. Temperature and salinity were determined from unpublished data held by the Centre for Environment, Fisheries and Aquaculture science (Cefas, Lowestoft, UK) and ICES (ICES, Copenhagen, Denmark). The sea area (Channel, North or Celtic), distance from nearest coast and a stratification parameter were calculated from latitude and longitude. The stratification parameter is on a linear scale and indicated the extent to which waters remain mixed throughout the year or stratify during summer (derived from the formulation presented in Pingree and Griffiths (1978) using modeled tidal velocities).

2.4. Data analysis

Since both scallops and fish will vary in lipid content in space and time, and since lipid $\delta^{13}C$ is highly depleted and can bias the interpretation of food web data (Focken and Becker, 1998), the C:N ratios determined during isotope analysis were used to mathematically correct the $\delta^{13}C$ values to lipid-free equivalents using the mass balance equation: