Ph-D position

ISIT_U: In search of isotopic uncertainties in ecology using food web dynamic modelling

1. Synopsis

Abstract

The present project deals with the improvement of a widely used tool in Ecology, i.e. stable isotope analysis (SIA), by a better understanding of the underlying mechanisms and by a greater account taken of its incorporation in trophic ecology. Living organisms interact by means of predator-prey relationships within food webs therefore controlling most ecological processes directly or indirectly. Improving SIA methods at different biological organisational levels allows to better monitor how global change affects biodiversity and ecosystem functioning (climate regulation, food supply etc…) in a multifactorial way. Primary focus will be on marine species and ecosystems but could be extended to terrestrial species and ecosystems for comparison purposes. For example, a database on marine and freshwater fishes has been already completed. The project is fundamental, yet the impact on the scientific community will be straight thanks to the development of R packages freely available.
Key words: Trophic ecology, dynamic modelling, stable isotopes, diet-switching experiment, trophic enrichment factor.

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Fundings :

The Ph-D is funded equally by Ifremer and university of Lille North Europe and is embedded in the project "Isit-U". Total funding is 250 k€ and will allow comfortable environment for the hired candidate (Publications, accommodations for participating at conferences or workshops etc…).

Host laboratories:

- Laboratory of Oceanography and Geosciences (UMR 8187 LOG CNRS, Lille, ULCO, Wimereux, France), website: http://log.cnrs.fr/
- Channel and North Sea Fisheries Research Unit (Ifremer, Boulogne-sur-mer, France) website: https://wwz.ifremer.fr/manchemerdunord/Unite-Halieutique/

Doctoral school:

ED 104 SMRE website http://edsmre.univ-lille1.fr/

Expected collaborations:
External collaborations are highly expected with:
-University of Wyoming (Laramie, United states, Pr C. Martinez Del Rio http://www.uwyo.edu/cmdelrio/site/welcome.html)
-Members of the GDR CNRS 3176 GRET (http://gdr-gret.univ-bpclermont.fr/) such as Laure Pecquerie, Stanislas Dubois, Carolina Giraldo...

Ultimately, a double doctorate (or a secondment period) is actually under consideration with US.

Position
A 3 year doctoral position will be available starting from October 2018. The salary is *ca* 1550 € per month before taxes (10% taxes on average). The PhD student will be responsible for setting up its own project within the scope of the Isit U project detailed below. The candidate will take over the responsibility of refining and/or developing models of isotopic incorporation at species and community levels. A research engineer will be hired to help the Ph-D student in data collection, data mining and friendly coding in R. The co-supervizing team gathers researchers from different disciplines in ecology (modelling, fisheries, trophic ecology…).

Profile
Applicants must hold a Master in ecology/biology and must show good skills in organizational aptitude, autonomy, capacity for synthesis (bibliography) and communication. We are looking for a highly motivated student. The candidate will have skills in numerical ecology, modelling (e.g. Individual based models, bioenergetics) and programming (e.g. C++, Java, R, Matlab) and affinities for trophic ecology. Fluent English will be appreciated.

Application
Please send to all supervisors until June 15, 2018:
(1) your detailed CV
(2) a pertinent letter of motivation
(3) the name and the coordinates of 2 scientific referents
(4) a copy of your grades (or scores) in first and second years of your master when availaible

Later applications will be considered if position has not been filled.

Skype interviews will be planed end of June

2. Detailed research proposal

Scientific background

The structure and functioning of food webs have been the subject of increasing interest during the past two decades (Dunne et al., 2009) to understand and to predict the response of ecosystems to environmental change (Woodward et al. 2010). In 2017, some 1.5% of papers in the field of ecology concerns trophic ecology, with an increase rate of 10% per year (Garvey and Whiles, 2017). Research questions on food web structure lie in the field of ecological networks that aims at understanding how community structure and trophic interactions affect ecosystem functioning (Ings et al., 2009). Studies on the structure and dynamic of food webs are thus essential to predict the response of ecosystems to the effect of global change on biodiversity (Duffy et al., 2007) from the individual to the community level (Keyl and Wolff 2008). Nevertheless, studies of trophic network structure at large spatial and taxonomical scales in ecosystems remain relatively scarce (Ings et al., 2009) and especially in marine ones (but see Woodland and Secor, 2013). However, the world ocean ecosystem delivers several critical ecosystem services to the human kinds such as climate regulation, food supply and water quality regulation. Trophic Ecology is then "pivotal" in ecology because it is underlying most ecological processes and questions. This field of research has been fostered by widely spread methods to measure assimilation and transfers of matter (e.g. stable isotopic analysis, SIA), and by a vast field of numerical approaches (e.g. dynamic modelling ….).

Ecologists have increasingly shown interest in SIA, to provide novel insights into the trophic ecology of animals and structure of food webs. Trophic relationships are not easily observable in nature and SIA allows estimating networks of trophic interactions quite easily. SIA have been used to trace pathways of organic matter into food webs, to examine intra- and inter-species trophic relationships, to track origins and migration of animals or to reconstruct organisms' diets (see review of Boecklen *et al.* 2011). The study of a large number of species, individuals within species, and food webs using SIA facilitates ecosystem comparison and meta-analysis using SIA-derived metrics (Fry and Davis, 2015, Layman et al., 2007). The decrease in analysis costs (typically 6 € for carbon and nitrogen analysis) and the ease to produce results have led to a specular bloom of the numbers of isotope studies: more than 5100 papers were published on this subject in 2016 (the increase rate is 5% per year). However, inferring properties from SIA to decipher trophic relationships lies on strong assumptions which have been questioned for 20 years (e.g. Martinez del Rio, 2009) and are now challenged using theoretical approaches (e.g. Jabot et al., 2017) and experimental approaches (e.g. Gorokhova, 2017).

Originality and innovative character of the project

Natural carbon and nitrogen stable isotope ratios in tissues of organisms closely resemble those in their diets when steady state (isotopic equilibrium) is reached after a certain time lag, but with slight enrichment, classically called trophic enrichment factor (TEF also noted Δ). TEF has long been recognized as a critical measurement to reconstruct diets and trophic web structure (Post 2002). TEF is explained by the fact that light isotopes (^{12}C, ^{14}N for carbon and nitrogen) are preferentially used versus heavier isotopes (^{13}C, ^{15}N) in catabolism, leading to enrichment in the tissues (Gannes *et al.* 1998, Martinez del Rio *et al.,* 2009). As stated by Philips & Koch (2002), "the weakest link in the application of mixing models to a dietary reconstruction relates to the estimation of appropriate Δ values". Later, Martinez del Rio *et al.* (2009) further drove the point home while writing about a "neglected complication". Another relevant aspect of the dynamics of isotopic incorporation is how fast an animal tissue reflects the isotopic composition of the diet, or "over what time period is resource use integrated" (i.e. the time lag here above, Vander Zanden *et al.* 2015). Incorporation dynamic of isotope from food is basically dependent on metabolism and is classically apprehended with the turnover rate (λ) defined as the incorporation rate of an element divided by the biomass of the element. λ is assumed to be the sum of the rate of tissue growth (i.e. net anabolism, or new biomass) and catabolism (i.e. tissue replacement; Hesslein *et al.* 1993, Vander Zanden *et al.* 2015). TEF and λ are the two critical aspects of isotopic dynamics

which are typically overviewed and neglected (Martinez del Rio *et al.* 2009, Lefebvre and Dubois, 2016).

Diet-switching experiments (DSE), in which animals are fed on isotopically constant food source over a time period, are one of the best (if not the only) way to estimate TEF and turnover rates. Different empirical models and equations were developed to interpret DSE and took into account tissue growth and catabolic turnover explicitly or implicitly (Fry and Arnold, 1982; Hobson and Clark, 1992; Hesslein et al., 1993; Carleton and Martinez del Rio, 2010). Notably, three components of these equations are by nature not constant. First, weight (and size) is not constant during the experiment since organisms grow. Furthermore, the growth does not always follow an exponential curve as assumed by these equations. Second, food isotope signatures (δ_f) is often inconstant particularly in experiment where live food is given to the consumers or when experiments last several months (large species). Third, there are accumulating evidences that TEF varies with growth and catabolism (e.g. Pecquerie et al., 2010; Lefebvre & Dubois, 2016; Gorokhova, 2017). In natural environments, growth, δ_f and TEF may vary substantially depending on ecological factors (such as T°, food availability etc...). Many DSE assume that these three components are constant which is obviously difficult to achieve. Another but recent way to do, is to further develop and use bioenergetical models integrating explicitly isotope dynamics (see Remien 2015, Pecquerie et al., 2010; Emmery et al., 2011). In this project, we will assume that isotopic equilibrium is never reached which is what most certainly happens in natural environments. The consequence of assuming that these parameters are constant is an incorrect assessment of TEF and turnover rates which may impair strongly the ecological properties inferred from the use of SIA.

The general aim of this thesis project is **to improve the use of SIA as a tool in ecology by a better understanding of the underlying mechanisms controlling TEF and turnover rates.** The tool being widely used at different organisational levels, the impact of dynamic TEF, turnover rate and food isotopes signatures will be measured at species level, population, community, food webs and finally ecosystem levels using dynamic modelling. When relevant, tools will be developed as R packages to be used by the scientific community.

Specific aims and methodological approaches are two folds:

Task 1: Species level

At the species but also individual levels, the ecological applications include reconstructing diet, tracing migratory routes or estimating physiological state. Here, evidences accumulate that TEF is relied to growth (Emmery et al., 2011) and incorporation rate is relied on bioenergetics and scale with size, food and temperature (Vander Zanden et al., 2015). Models usually used to estimate TEF and incorporation rates in DSE were originally statistically-derived and used to fit phenomenon (see Hesslein et al., 1993): they are empirical by nature, and are typically static concerning TEF, λ and δ_f. On the opposite, pure mechanistic models were developed recently (see Remien 2015, Pecquerie et al., 2010; Emmery et al., 2011) but appear too complex to be used generally by average trophic ecologists. First (subtask 1.1), a new model will be developed by simplifying complex mechanistic approaches and applied on published and unpublished diet-switch experiments (DSE). This model will take into account all dynamics of DSE (incorporation rates, food signatures, and TEF) and will be implemented in R and published on Github. New estimations of TEF and incorporation rate will be then compared to published ones (separated experiments and meta-analysis Vander Zanden et al., 2015). In parallel of the thesis work (I site ULNE project), the use of isotopic DEB in its full version (DIB; Pecquerie et al., 2010) is planned to challenge the new model. Focus species would be aquatic, e.g. bivalves and fish. Second (sub task 1.2), the consequences of incorporating dynamics on diet estimation will be evaluated by coupling the new model with mixing Bayesian models (Parnell et al., 2010). Published results in the field will then be revisited.

Task 2: Population, community and food web level

At these levels, the ecological applications are evaluating the trophic niche of a species or the intra- and inter-competition for food, and evaluating the diversity of food sources used by the food web, and the network of trophic interactions (Layman et al., 2012). The use of two or three natural isotopes allows to generate isotopic spaces for these purposes. Using a theoretical approach (the so-called Niche Model, Williams and Martinez, 2000), Jabot et al (2017) were the firsts to challenge the use of isotopic inferences in food web ecology. They showed that grasping subtle patterns of food web structure using these inferences could be quite unrealistic for many food

webs and possibly marine ecosystems. Marine trophic networks are complex and their biological diversity is high. Concomitantly with these natural features, human impacts are of different nature and interact in synergy. For example, climate change or eutrophication drives marine food webs and fisheries by bottom-up effect (Beaugrand, 2004). The other way round, fisheries and overexploitation induce trophic cascade by elimination of top predators and impact lower trophic levels and water quality via a top down effect (Casini et al., 2008). These multifactorial effects are taken into account by end-to-end dynamic ecosystem models developed at Ifremer such as OSMOSE (Travers-Trolet et al., 2014). An interesting feature of OSMOSE is the modelling of individual-based response of several fish species, the food web being structured by mechanistic laws (i.e. opportunistic and size-based trophic interactions). OSMOSE (coupled to a NPZD model as in Travers et al., in preparation) is then an ideal tool to implement mechanistic isotopic properties (variable TEFs vs dynamic incorporation rates). In sub-task 2.1, isotopic properties and dynamics will be implemented in OSMOSE, based on the simple mechanistic model developed in task 1. Modelled isotope outputs at the food web level will then be compared to published results in the English Channel (Kopp et al., 2015; Giraldo et al., 2017). The final aim is to test the possibility to inverse the paradigm of the classical use of isotope: isotopes will not be used anymore at the data-level to infer properties on food web but rather, raw isotope signatures will be modelled by OSMOSE and directly compared to observations. In sub task 2.2, OSMOSE will be used to test the robustness of SIA and their metrics to picture the effect of human impacts (climate change, eutrophication, and overexploitation) following the philosophy of Jabot et al. (2017).

Expected impacts
The project has the ambition to improve the use of a widely applied tool (SIA) in ecology and to evaluate the uncertainty of its inferences and metrics at different organisational levels (population, community and ecosystem). The main aim is not "to upturn the tea table" but rather to sustain objectively the strengths and weaknesses of SIA in ecology. It is highly expected that the use of these inferences and metrics is probably irrelevant in some ecosystems (as shown by Jabot et al., 2017) without prior in depth understanding and quantification of fundamental processes (dynamic TEF and incorporation rates) that the project aims to identify and to unravel. Impacts on the scientific community would be high by providing new insights in this growing ecological field and also by providing new recipes under R packages to better decipher food web structure, a fundamental prerequisite to understand global change effects on biodiversity and ecosystem functions. Top ten % peer reviewed journal in ecology will be targeted to disseminate each of the sub-task as we have already done (see Jabot et al 2017 in Funct. Ecol. or Giraldo et al., 2017 in Limnol. & Oceanogr.) or trying to do presently (American naturalist, Methods in Ecology and Evolution).

Forward schedule

References

Beaugrand, G., 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. Progress in Oceanography. 60, 245-262.

Boecklen, W.J., Yarnes, C.T., Cook, B.A., James, A.C., 2011. On the Use of Stable Isotopes in Trophic Ecology. in: Futuyma, D.J., Shaffer, H.B., Simberloff, D. (Eds.), Annual Review of Ecology, Evolution, and Systematics, Vol 42, pp. 411-440.

Carleton, S.A., del Rio, C.M., 2010. Growth and catabolism in isotopic incorporation: a new formulation and experimental data. Functional Ecology. 24, 805-812.

Casini, M., Lovgren, J., Hjelm, J., Cardinale, M., Molinero, J.-C., Kornilovs, G., 2008. Multi-level trophic cascades in a heavily exploited open marine ecosystem. Proceedings of the Royal Society B-Biological Sciences. 275, 1793-1801.

Dunne, J.A., Williams, R.J., 2009. Cascading extinctions and community collapse in model food webs. Philosophical Transactions of the Royal Society B-Biological Sciences. 364, 1711-1723.

Emmery, A., Lefebvre, S., Alunno-Bruscia, M., Kooijman, S.A.L.M., 2011. Understanding the dynamics of delta(13)C and delta(15)N in soft tissues of the bivalve Crassostrea gigas facing environmental fluctuations in the context of Dynamic Energy Budgets (DEB). Journal of Sea Research. 66, 361-371.

Fry, B., Arnold, C., 1982. RAPID C-13/C-12 TURNOVER DURING GROWTH OF BROWN SHRIMP (PENAEUS-AZTECUS). Oecologia. 54, 200-204.

Fry, B., Davis, J., 2015. Rescaling stable isotope data for standardized evaluations of food webs and species niches. Marine Ecology Progress Series. 528, 7-17.

Gannes, L.Z., del Rio, C.M., Koch, P., 1998. Natural abundance variations in stable isotopes and their potential uses in animal physiological ecology. Comparative Biochemistry and Physiology a-Molecular and Integrative Physiology. 119, 725-737.

Giraldo, C., Ernande, B., Cresson, P., Kopp, D., Cachera, M., Travers-Trolet, M., Lefebvre, S., 2017. Depth gradient in the resource use of a fish community from a semi-enclosed sea. Limnology and Oceanography. 62, 2213-2226.

Gorokhova, E., 2017. Shifts in rotifer life history in response to stable isotope enrichment: testing theories of isotope effects on organismal growth. Royal Society Open Science. 4.

Hesslein, R.H., Hallard, K.A., Ramlal, P., 1993. REPLACEMENT OF SULFUR, CARBON, AND NITROGEN IN TISSUE OF GROWING BROAD WHITEFISH (COREGONUS-NASUS) IN RESPONSE TO A CHANGE IN DIET TRACED BY DELTA-S-34, DELTA-C-13 AND DELTA-N-15. Canadian Journal of Fisheries and Aquatic Sciences. 50, 2071-2076.

Hobson, K.A., Clark, R.G., 1992. ASSESSING AVIAN DIETS USING STABLE ISOTOPES .2. FACTORS INFLUENCING DIET-TISSUE FRACTIONATION. Condor. 94, 189-197.

Ings, T.C., Montoya, J.M., Bascompte, J., Bluethgen, N., Brown, L., Dormann, C.F., Edwards, F., Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., Ledger, M.E., Lewis, H.M., Olesen, J.M., van Veen, F.J.F., Warren, P.H., Woodward, G., 2009. Ecological networks - beyond food webs. Journal of Animal Ecology. 78, 253-269.

Jabot, F., Giraldo, C., Lefebvre, S., Dubois, S., 2017. Are food web structures well represented in isotopic spaces? Functional Ecology. 31, 1975-1984.

Keyl, F., Wolff, M., 2008. Environmental variability and fisheries: what can models do? Reviews in Fish Biology and Fisheries. 18, 273-299.

Kopp, D., Lefebvre, S., Cachera, M., Villanueva, M.C., Ernande, B., 2015. Reorganization of a marine trophic network along an inshore-offshore gradient due to stronger pelagic-benthic coupling in coastal areas. Progress in Oceanography. 130, 157-171.

Layman, C.A., Arrington, D.A., Montana, C.G., Post, D.M., 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology. 88, 42-48.

Layman, C.A., Araujo, M.S., Boucek, R., Hammerschlag-Peyer, C.M., Harrison, E., Jud, Z.R., Matich, P., Rosenblatt, A.E., Vaudo, J.J., Yeager, L.A., Post, D.M., Bearhop, S., 2012. Applying stable isotopes to examine food-web structure: an overview of analytical tools. Biological Reviews. 87, 545-562.

Lefebvre, S., Dubois, S.F., 2016. THE STONY ROAD TO UNDERSTAND ISOTOPIC ENRICHMENT AND TURNOVER RATES : INSIGHT INTO THE METABOLIC PART. Vie Et Milieu-Life and Environment. 66, 305-314.

Martinez del Rio, C., Wolf, N., Carleton, S.A., Gannes, L.Z., 2009. Isotopic ecology ten years after a call for more laboratory experiments. Biological Reviews. 84, 91-111.

Parnell, A.C., Inger, R., Bearhop, S., Jackson, A.L., 2010. Source Partitioning Using Stable Isotopes: Coping with Too Much Variation. Plos One. 5.

Pecquerie, L., Nisbet, R.M., Fablet, R., Lorrain, A., Kooijman, S.A.L.M., 2010. The impact of metabolism on stable isotope dynamics: a theoretical framework. Philosophical Transactions of the Royal Society B-Biological Sciences. 365, 3455-3468.

Phillips, D.L., Koch, P.L., 2002. Incorporating concentration dependence in stable isotope mixing models. Oecologia. 130, 114-125.

Post, D.M., 2002. The long and short of food-chain length. Trends in Ecology & Evolution. 17, 269-277.

Remien, C.H., 2015. Modeling the dynamics of stable isotope tissue-diet enrichment. Journal of Theoretical Biology. 367, 14-20.

Vander Zanden, M.J., Clayton, M.K., Moody, E.K., Solomon, C.T., Weidel, B.C., 2015. Stable Isotope Turnover and Half-Life in Animal Tissues: A Literature Synthesis. Plos One. 10.

Williams, R.J., Martinez, N.D., 2000. Simple rules yield complex food webs. Nature. 404, 180-183.

Woodland, R.J., Secor, D.H., 2013. Benthic-pelagic coupling in a temperate inner continental shelf fish assemblage. Limnology and Oceanography. 58, 966-976.

Woodward, G., Blanchard, J., Lauridsen, R.B., Edwards, F.K., Jones, J.I., Figueroa, D., Warren, P.H., Petchey, O.L., 2010. Individual-Based Food Webs: Species Identity, Body Size and Sampling Effects. in: Woodward, G. (Ed.), Advances in Ecological Research, Vol 43: Integrative Ecology: from Molecules to Ecosystems, pp. 211-266.