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Implications of morphological and functional traits for trophic relationships within fish communities and marine trophic network architecture

Implications des traits morphologiques et fonctionnels pour les relations trophiques dans les communautés de poissons et l'architecture du réseau trophique marin


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Résumé court

Implications des traits morphologiques et fonctionnels pour les relations trophiques dans les communautés de poissons et l'architecture du réseau trophique marin.

Un thème actuel en écologie est de comprendre la contribution de la biodiversité au fonctionnement des écosystèmes, notamment comment la variation inter- et intra-spécifique des traits affecte les interactions trophiques, l'organisation trophique des communautés, et l'architecture des réseaux trophiques. Historiquement, la morphologie a été considérée comme un déterminant majeur de l'écologie des organismes et, dans une perspective fonctionnelle, est supposée influencer les relations trophiques et les autres fonctions écologiques des espèces.

Cette thèse visait à étudier l'organisation trophique d'une communauté de poissons marins et sa relation avec la variation intra- et inter-spécifique des traits morphologiques et fonctionnels. Le réseau trophique associé dévoile une structure en méta-communauté comprenant deux sous-réseaux le long du gradient côte-large. La largeur de la niche trophique spécifique croit avec la variation de la niche trophique individuelle, un patron en partie lié à l'identité fonctionnelle des espèces et au sexe, à la taille et à l'habitat des individus. La morphologie des espèces, non leur phylogénie, se révèle un indicateur parfait de leur identité fonctionnelle. Enfin, la morphologie parait être la principale source de variabilité des relations trophiques individuelles dans l'assemblage mais une large part de variation inexpliquée suggère l'omission de facteurs cruciaux, dont le comportement. Ces résultats permettent de mieux comprendre le rôle de la diversité morphologique et fonctionnelle sur la structure des réseaux trophiques marins et pourraient aider à prédire leurs dynamiques spatio-temporelles ainsi que leurs réponses aux perturbations.

Mots-clés: communauté, morphologie, réseau trophique, niche, traits fonctionnels, Manche Est

Resumé long

Implications des traits morphologiques et fonctionnels pour les relations trophiques dans les communautés de poissons et l'architecture du réseau trophique marin.

Un des principaux buts de l'écologie est de comprendre comment la biodiversité contribue au fonctionnement des écosystèmes. La littérature croissante sur le sujet soulève, entre autres, l'importance de l'interaction entre variation individuelle (intraspécifique) et interspécifique des traits pour la structure et la dynamique des populations, des communautés et des écosystèmes.

Une façon intéressante de faire le lien entre diversité des traits et fonctionnement des écosystèmes est d'utiliser une approche trophique. Puisque les réseaux trophiques cartographient l'ensemble des interactions trophiques entre individus et entre espèces, leur structure et leur dynamique devraient être affectés par les variations intra- et inter-spécifiques des traits. Parallèlement, ils sont impliqués dans l'un des processus principaux des écosystèmes, le transfert d'énergie et de biomasse entre les espèces, et constituent une voie de propagation privilégiée pour les perturbations à travers les cascades trophiques. Dans l'optique de comprendre le lien entre biodiversité et fonctionnement des écosystèmes, il est donc important d'appréhender comment la variation des traits peut influencer les relations trophiques, l'organisation trophique des communautés, et l'architecture des réseaux trophiques résultants. Plus particulièrement, la morphologie parmi d'autres traits a été historiquement considérée comme un déterminant majeur de l'écologie des organismes, ce qui a mené au développement de l'écomorphologie (lien écologie-morphologie). Dans la perspective fonctionnelle actuelle, la morphologie est supposée être impliquée dans les relations trophiques et les fonctions écologiques assumées par les espèces.

Prenant comme cas d'étude la communauté ichtyologique de Manche Est, cette thèse avait pour but d'étudier l'organisation trophique d'une communauté animale et comment elle dépend des variations des traits morphologiques et fonctionnels entre les espèces et au sein des espèces. Un préambule nécessaire était tout d'abord d'établir la structure du réseau trophique de la communauté de poissons de la Manche orientale. Dans un second temps, les implications des caractéristiques trophiques des espèces, de leurs traits fonctionnels, et des variations individuelles de régime alimentaire pour l'organisation trophique des espèces de la communauté de poissons ont été étudiées. Troisièmement, les relations entre les caractéristiques morphologiques des espèces d'une part et leurs traits fonctionnels ainsi que leur proximité phylogénétique d'autre part ont été considérées. L'influence des variations morphologiques individuelles sur les caractéristiques de la niche morphologique des espèces a également été estimée. Finalement, les implications directes de la phylogénie, de la morphologie, de l'habitat et des variables d'état individuel sur les relations trophiques dans l'assemblage de poissons ont été étudiées.

Les quatre études ont été basées sur 853 individus échantillonnés au sein de seize espèces de poissons (Teleosteii and Elasmobranchii) choisies pour leur représentativité de la communauté ichtyologique de Manche orientale et collectés sur une centaine de stations au cours de la campagne CGFS (Channel Ground Fish Survey) opérée par IFREMER en Octobre 2009.

L'exploration de la structure du réseau trophique sous-tendu par la communauté ichtyologique s'est appuyée sur la détermination des contenus des tractus digestifs et les analyses de réseaux dérivées de la théorie des graphes. Une structure hiérarchisée suivant un patron de métacommunauté comprenant deux sous-réseaux spatialement discriminés le long d'un gradient côte-large et liés par des espèces mobiles de haut niveaux trophiques a été détecté. Tandis que les changements ontogéniques de niche sont apparus comme un déterminant mineur de la structure du réseau trophique, les implications majeures de la composition spécifique de la communauté (biodiversité) et de l'identité trophique des espèces en particulier ont été mises en lumière.

L'étude de l'organisation trophique de la communauté ichtyologique a reposé sur l'analyse des contenus des tractus digestifs. Elle avait pour but de tester la « Niche Variation Hypothesis » (NVH; Van Valen, 1965) appliquée à la niche trophique des espèces au sein de la communauté ichtyologique ainsi que d'examiner ses liens avec la compétition inter-spécifique potentielle (chevauchement de niches) et avec les attributs fonctionnels des espèces (liés à l'habitat et la stratégie de nourrissage). Une corrélation positive entre la largeur de la niche trophique des espèces et le niveau de variation de régime alimentaire entre individus supportant la NVH a été observée, mais ni le patron actuel de compétition entre espèces (chevauchement de niches) ni les attributs fonctionels des espèces n'étaient liés à leur largeur de niche. L'affiliation des espèces à un groupe fonctionnel (i.e. identité fonctionnelle telle que petits pélagiques ou prédateurs diurnes démersaux par exemple) est cependant apparue en partie liée à certaines de leurs caractéristiques de niche trophique. Une diversité de patrons d'occupation individuelle de la niche trophique des espèces a été détectée (individus distribués au hasard, surdispersés ou groupés). Certains patrons groupés ont pu être, pour quatre espèces, reliés à des différences inter-individuelles d'habitat, de sexe ou de taille corporelle.

L’étude morphologique de la communauté de poissons s’est basée sur une approche géomorphométrique utilisant l’analyse Procrustes 2D de points de repère homologues entre espèces et définis pour décrire au mieux la forme générale du corps des individus. Ce chapitre est basé sur l’idée que la niche morphologique d’une espèce peut être utilisée comme reflet de sa niche écologique. Il visait à évaluer à quel point la diversité morphologique de la communauté peut être liée à sa diversité phylogénétique et à sa diversité fonctionnelle ainsi qu’à tester la NVH appliquée aux niches morphologiques des espèces de la communauté. La diversité phylogénétique n’est pas apparue pertinente pour décrire la diversité morphologique de l’assemblage, tandis qu’une adéquation étroite entre diversité morphologique et diversité fonctionnelle des espèces a été observée. De façon surprenante, la NVH n’a pas été supportée pour la niche morphologique, la largeur de la niche trophique des espèces n’étant pas corrélée au niveau de variation morphologique individuelle.

La dernière étape de cette thèse a été d’identifier les déterminants principaux des relations trophiques dans la communauté de poissons, par l’évaluation des contributions relatives de la diversité phylogénétique, morphologique, et d’habitat ainsi que de la variabilité des états individuels à la variation individuelle de régime alimentaire au sein de la communauté. Il est apparu que la morphologie est le principal facteur expliquant la variabilité des relations trophiques, avec 25% de la variation expliquée. Les 75% de variation non expliqués suggèrent que d’importantes sources de variation du régime alimentaire ont été négligées. Une source de variation alimentaire relativement évidente est le comportement, qui peut être très important puisque les poissons sont bien connus pour leur versatilité alimentaire. Leur capacité à changer leur comportement alimentaire et ses conséquences sur le fonctionnement des écosystèmes seraient intéressants à considérer pour des recherches futures.

Pris dans leur ensemble, ces résultats pourraient permettre de mieux comprendre le role de la diversité sur la structure des réseaux trophiques marins et potentiellement aider à prédire leurs dynamiques spatio-temporelles ainsi que leurs réponses aux perturbations.

Mots-clés: communauté, morphologie, réseau trophique, niche, traits fonctionels, Manche Est.

Josette Cachera

Short abstract

Implications of morphological and functional traits for trophic relationships within fish communities and marine trophic network architecture.

A current issue in ecology is to understand the contribution of biodiversity to ecosystem functioning and notably to comprehend how inter- and intra-specific trait variation affects trophic interactions between individuals and species, the trophic organization of communities and trophic network architecture. Particularly, morphology has historically been considered as a main determinant of organisms' ecology, which led to the field of ecomorphology, and, from a functional perspective, is expected to influence trophic relationships and other ecological functions performed by species.

This thesis aimed at studying the trophic organization of a marine fish community and its dependency on morphological and functional trait variation between and within species. The associated trophic network revealed a meta-community structure, including two sub-networks along a coastal-offshore gradient. Species trophic niche breadth and individual trophic niche variation increased together, a pattern relying partly on species functional identity and the sex, body size and habitat of individuals. Contrary to phylogeny, species morphology was a relevant proxy for functional identity. Finally, morphology seemed the main source of variability in individual trophic relationships within the assemblage, but a large part of diet variation remained unexplained suggesting that critical factors had been neglected, notably behaviour. These results allow understanding better the role of morphological and functional diversity in the structure of marine trophic networks and may help to predict their spatio-temporal dynamics and their responses to perturbations.

Keywords: community, morphology, trophic network, niche, functional traits, eastern English Channel

Long abstract

Implications of morphological and functional traits for trophic relationships within fish communities and marine trophic network architecture.

A main goal in ecology is to understand the contribution of biodiversity to ecosystem functioning. The growing literature addressing this issue points out, among others, the importance of the interplay between individual (intra-specific) and inter-specific trait variation on the structure and dynamics of populations, communities and ecosystems.

An interesting way to link trait diversity with ecosystem functioning is to use a trophic approach. Since trophic networks (food webs) map the trophic interactions between individuals and between species, their structure and dynamics may be affected by intra- and inter-specific variation in traits. In addition, trophic networks underlie one of main processes in ecosystems, namely energy and mass transfers across species and are particular pathways for perturbation propagation through trophic cascades. Consequently, it is important for our knowledge of the influence of biodiversity on ecosystem functioning to understand how trait variation affects trophic relationships, trophic organization of communities and the resulting architecture of trophic network. Particularly, morphology among other traits has historically been considered as a main determinant of organisms' ecology, leading to the field of ecomorphology, and, from the current functional perspective, is expected to be involved in trophic relationships and the ecological functions performed by species.

Based on the fish community of the eastern English Channel taken as a case study, this PhD thesis aimed at studying trophic organization within animal communities and its dependency on morphological and functional traits variation between and within species. A necessary preamble was first to establish the structure of the trophic network involving the fish community of the eastern English Channel. In a second step, the implications of species trophic characteristics, functional traits related mainly to habitat and foraging strategy, and individual diet variation for the trophic organization of the fish community were studied. Third, the relationships between species morphological characteristics on the one hand and functional traits as well as phylogenetic proximity on the other hand were considered. The influence of morphological variation among conspecifics on species morphological niche characteristics was also studied. Finally, the direct implications of phylogeny, morphology, habitat and individual state for trophic relationships in the whole fish assemblage were investigated.

All four studies were based on 853 individuals sampled from sixteen fish species (Teleosteii and Elasmobranchii) that were chosen for their representativeness of the eastern English Channel fish community and that were collected at almost 100 sampling sites during the Channel Ground Fish Survey operated by IFREMER in October 2009.

The exploration of the structure of the trophic network underlay by the fish community was based on digestive tract content determination and network analysis derived from graph theory. A hierarchical architecture based on a metacommunity pattern was detected with spatially-discriminated sub-networks along the seaward gradient, one offshore and one coastal, linked by mobile high-trophic-level species. Whereas ontogenetic niche shift appeared only as a minor determinant of the trophic network structure, the main implication of community composition, and thus biodiversity, and of species trophic identity in particular was highlighted.

The study of the fish community trophic organization was based on digestive tract content analysis and aimed to test the Niche Variation Hypothesis (NVH; Van Valen, 1965) applied to species trophic niche within the community, as well as to investigate its links with potential inter-specific competition (niche overlap) and species functional attributes (related to habitat and foraging strategy). The NVH was successfully supported by a positive correlation between species trophic niche breadth and individual diet variation, but appeared neither related to the current pattern of inter-specific competition (niche overlap) nor to species functional attributes. Species affiliation to a functional group (i.e. functional identity such as small pelagic, diurnal demersal foragers), however, appeared to be somewhat linked to trophic niche characteristics. A diversity of patterns of individual occupation of species trophic niches was detected (individuals' distribution being overdispersed, random or clustered). For four species, clustered patterns were apparently explained by inter-individual differences in habitat and/or body size.

The morphological study of the fish community was based on a geomorphometric approach and used 2-D Procrustes analysis of homologous landmarks across species defined to describe the general body shape of individuals. This chapter relied on the idea that a species' morphological niche can be used as surrogate of its ecological niche and aimed to test whether the morphological diversity of the community was related to species phylogenetic and/or functional diversity, as well as whether the Niche Variation Hypothesis applied to species morphological niches within the community. Phylogenetic diversity appeared irrelevant to assess the morphological diversity of the assemblage whereas the diversity of species body shapes matched perfectly their functional diversity. Surprisingly, the NVH was

not supported for the morphological niche, species trophic niche breadth being unrelated to individual morphological variation.

The final step of this thesis was to identify the main determinants of trophic relationships in the fish community by assessing the relative contributions of phylogenetic, morphological, and habitat diversity as well as individual state variation to variability in individuals' diet within the community. It appeared that morphology was the principal factor explaining variability in trophic relationships with 25 % of variation explained. The unexplained 75 % of variation suggest that some other important sources of variation in diet have been neglected. A relatively obvious one is behavior and its associated diversity, which may be all the more relevant since fish are well known for their feeding versatility. Their ability to switch foraging behavior and the consequences of such capacity on ecosystem functioning may thus be particularly interesting to consider for future research.

Taken altogether, these results may further allow understanding better the role of diversity on the structure of marine trophic networks and potentially predicting its spatio-temporal dynamics and its responses to perturbations.

Keywords: community, morphology, trophic network, niche, functional traits, eastern English Channel.

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A chinchard féroce et Nico, bande de malades, ça va me manquer de ne pas être en mer avec vous. Je signe quand vous voulez pour une nouvelle CGFS !
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"So raise your glass if you are wrong
In all the right ways
All my underdogs, we will never, never be
Anything but loud and nitty gritty,
Dirty little freaks"

(P!nk, *Raise your glass*)

A **Franck**, pour ton soutien qui m'a été indispensable**.**

"Nous les écorchés vifs
On en a des sévices.
Oh mais non rien de grave
Y'a nos hématomes crochus qui nous sauvent
Et tous nos points communs
Dans les dents
Et nos lambeaux de peau
Qu'on retrouve ça et là"

(Noir Désir, *les Ecorchés*)

Pour **Wilfrid et Benoit**, pour nos discussions.

“Pour triompher, le mal n’a besoin que de l’inaction des homme de bien.”

(Edmund Burke)

A **Karine**, pour ta douce folie.

“But we're never gonna survive
Mais nous ne survivrons jamais

Unless we get a little crazy
Sauf si nous sommes un peu fou”

(Alanis Morissette, *Crazy*)

Pour mes p’tits vieux (**Yves, Franck (encore) et Jean-Paul petit poids**), faites sortir un peu votre côté rebelle !

“Ouvrier l'ombre est le cœur de nos vies
Qu'on a laissé saigner dans le fond des gouttières
Toujours sur les avenues
Les révolutionnaires tendent la main
A des gens qui n'en pensent pas moins”

(Saez, *Ma petite couturière*)

Pour **Sophie et Aurore**, n’oubliez jamais ça les filles :

“Truth passes through three phases:
La vérité passe par 3 phases:
First it is ridiculed
Premièrement elle est ridiculisée
Second, it is fiercely and violently opposed
Deuxièmement elle est contestée et violemment opposée,
Third, it becomes self-evident
Troisièmement, elle devient évidente”

(Arthur Schopenhauer)

A **Manu** (pour les heures (hilares) en labo, dédicaces de Frisette et Frisotte)

“-Tu n’es qu’un sale crétin
-Et toi une idiote
-Ta bouche sent le purin
-Tes yeux puent la crotte
-Schlounga ! ”

(Oldelaf, *Parce qu’on est jeune*)

A **Sylvie**, une des plus personnes les plus nobles que je connaisse.

“La gentillesse est la noblesse de l’intelligence”

Jacques Weber

A **Kelig**, pour ton aide, pour ton amitié

“*L'amitié c'est pour moi un paysage*
Où tu viens effacer mes petits nuages”

(Bernard Sauva, *L’amitié*)

Aux pepettes (**Mathilde, Gaelle, Flo, Coco, Béné et Brigitte**), pour être telles que vous êtes.

“Man kann von uns halten
On peut penser de nous

Was immer man da will
Toujours ce qu'on veut

Wir halten uns schadlos
Nous restons sans dommages

Wir halten niemals still
Nous ne nous tenons jamais tranquille”

(Rammstein, *Haifisch*)

Pour **Mickael**, merci pour ton aide et ton affreuse grammaire !

“Si il y a des vies qui vous sont chères pour nous elles le sont toutes”

(Bataillon des marins-pompiers de Marseille)

Pour **Elise**, pour ton soutien.

You need to find out
Cause no one's gonna tell you what I'm on about
You need to find a way for what you want to say

(Oasis, *Supersonic*)

A **Tataclé**, pour les années de conneries.

“Négatif, je suis une mite en pull over”
“Negative, I am a meat Popsicle”

(Korben Dallas, *The fifth element*)

Aux **anims de Jaures**, merci pour m’avoir montré que l’esprit d’équipe, ça existe en vrai.

“Wir halten zusammen
Nous sommes solidaires

Wir halten miteinander aus
Nous nous supportons

Wir halten zueinander
Nous sommes complices

Niemand hält uns auf
Personne ne nous arrête”

(Rammstein, *Haifisch*)

Pour **M. Quesroy et Mme Fougeron**, Danke für alles.

“Wir waren namenlos
Wir haben einen Namen
Waren wortlos
Die Worte kamen”

(Rammstein, *Los*)

A **Enora**, pour le temps passé et autant de souvenirs.

“Pour entretenir des amitiés solides, il ne suffit pas d’apprécier nos ressemblances, il faut aussi célébrer nos différences.”

James Fredericks

A **Cissou et Jo**, potesse de galère de thèse, et pote de galère de chômage.

“Qu'il est loin mon pays, qu'il est loin
Parfois au fond de moi se raniment
L'eau verte du canal du Midi
Et la brique rouge des Minimes
O mon païs, ô Toulouse, ô Toulouse”

(Claude Nougaro, *Toulouse*)

A **chatelaine et chatelain**, parce qu’ «on les brûle» !

“Je saurai recevoir je peux lui en faire voir de la sérénité
Et même lui laisser un certain goût de fer
Et ce bouquet de nerfs”

(Noir Désir, *Bouquet de nerfs*)

Pour les garçons, **Sébastien et Bruno**, merci d'être vous, merci de m'apprendre, merci de me supporter, merci de m'avoir écoutée des fois et toujours respectée, merci ☺

"Some kind of magic
Happens late at night
When the moon smiles down on me
And bathes me in it's light

It's a brand new day
The sun is shinning
It's a brand new day
For the first time
In such a long long time
I know
I'll be ok"

(Johua Radin, *Brand new day*)

A **mon Promis**

"Wanna stay right here,
Till the end of time, till the Earth stops turning
Gonna love you till the seas run dry
I've found the one I've waited for,
You're the one I've waited for"

(Lamb, *Gorecki*)

Pour **mes parents**, pour leur soutien inconditionnel, je vous aime.

"Ce n'est pas pour rien que les bébés qui viennent au monde naissent avec les poings fermés: ils savent déjà instinctivement qu'ils auront à lutter."

(Jean-Michel Wyl, *L'Exil*)

Knock the world right off its feet
And straight onto its head

(Red Hot Chili Peppers, *She's only 18*)

A mes parents, à mon Antoine

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Chapter I Synthesis

Josette Cachera

I.1 From niche to ecosystem functioning and biodiversity

I.1.1 At the very basis is the niche

The niche is a fundamental concept in ecology (Leibold 1995) but it is a term that defies definition, mainly because, originally, there were two distinct schools of thoughts regarding the niche concept (**Fig. I.1**). The first approach is founded on the work of Elton (1927) who defined the niche of a species as its role in the community and, by extension, its impacts on the environment. This school of thought ultimately led to the functional perspective of the niche. The second one originates in the work of Grinnell (1917) who described the niche as the set of environmental conditions a species need to persist, i.e. necessary for individuals to survive and produce offspring. It eventually evolved towards Hutchison's definition of the fundamental niche (Hutchinson 1957), i.e. the hypervolume a species occupies in an *n*-dimensional space, each dimension corresponding to a limiting factor (abiotic and biotic conditions, often and hereafter referred to as resources) for the capability of individuals to survive and reproduce in the absence of other species. Beyond this cleavage, Hutchinson's definition was considered as revolutionary in ecology, mainly because it specified two additional aspects of the niche: (i) the potential niche, i.e. the part of the fundamental niche that truly exists in geographical space and time, and (ii) the realized niche, i.e. the part of the potential niche a species is forced to occupy due to biotic interactions.

A major progress regarding the niche concept was achieved by developing a community approach. Wondering how similar species can coexist and which rules govern assembly in natural community, Gause (1936) proposed the principle of competitive exclusion, i.e. the fact that two species cannot coexist if they share a single niche. Years later, Gause's principle was completed by the work of MacArthur & Levins (1967) and MacArthur (1969) who developed the niche theory that defines important niche-related concepts, namely niche breadth (resources used by the species), niche partitioning (differential resources used by coexisting species), niche overlap (common resources used by coexisting species) and niche assembly (organization of species, **Fig. I.1**).

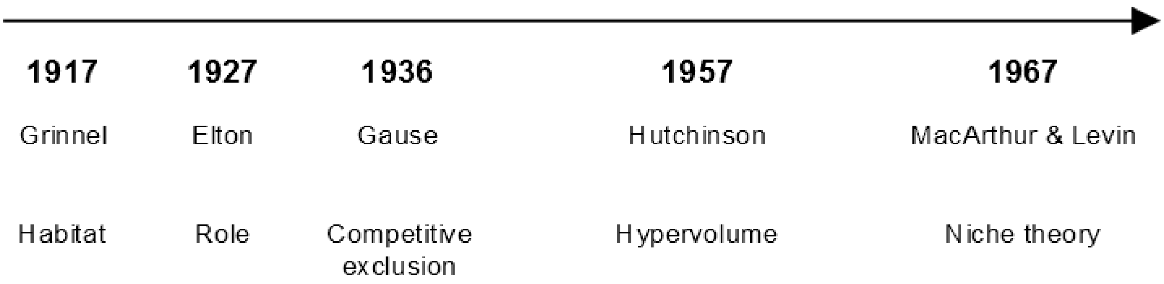


Figure I.1: Timeline of major advances in the concept of niche (not scaled but adapted from Chase & Leibold 2003).

I.1.2 From niche to ecosystem

Glossary

Complexity: environmental phenomena characterized by an organized structure and high variability.
Biodiversity: number and composition in terms of genotypes, species, functional types and landscape units of a given system (population, community, ecosystem…).
Function: organism responses to the environment and its effects on ecosystem functioning.
Functional trait: component of an organism's phenotype that influences ecosystem's properties (be it in the sense of response to the environment or effect on ecosystem functioning).
Ecosystem functioning: processes and properties of an ecosystem.
Ecosystem processes: geochemical cycling, mass and energy transfer, and other fluxes (e.g. water cycling).
Ecosystem properties: stability, hysteresis, irreversibility.
Stability: resistance (ability to stay in the same state despite a perturbation) and resilience (ability to return to its former state after a perturbation) of an ecosystem.
Hysteresis: pattern of recovery of an ecosystem after a perturbation.
Irreversibility: property of a state from which the ecosystem cannot escape no matter what action is taken.

Nowadays, the concept of niche remains essential since it is central in two main fields of research in ecology: (i) the puzzle of community assembly rules and organization and (ii) the responses of ecosystems to rapid environmental changes and their prediction (Holt 2009). These two issues have contributed to the development of functional ecology, which focuses on assessing the role of biodiversity on ecosystem processes and properties by identifying functions performed by species, particularly those threatened by extinction (Duffy 2003). This part of functional ecology is dealing with the understanding of the ecological role of organisms and thus concerns their "functional effect", i.e. the effect of species on ecosystem processes and properties (Petchey & Gaston 2006). It has to be distinguished from the functional classification of species according to their "functional response", i.e. the response of species to their abiotic and/or biotic environment (Hooper *et al.* 2002; Naeem & Wright

2003). Here, we will focus on the influence of biodiversity on ecosystem functioning through the functional effect of organisms or species (**Fig. I.2**) or, in other words on the relative contribution of functional diversity to ecosystem functioning (Sutherland *et al.* 2013).

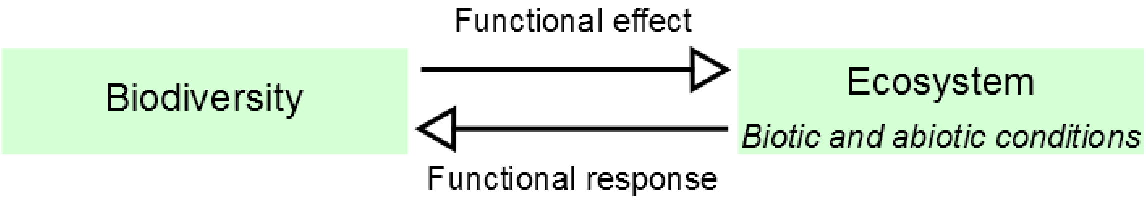


Figure I.2: Relationships between ecosystem and organisms from a functional point of view.

I.1.3 Ecosystem functioning, biodiversity and species functions

The question about the contribution of biodiversity to ecosystem functioning motivated the development of the Biodiversity Ecosystem Functioning (BEF) theory. It was originally based on the idea that the niches of species within a community are complementary, following the principle of niche partitioning, and thus that their functions might also be complementary. It is therefore intuitively expected that the more structured and variable environmental conditions are (complexity), the more species can coexists (biodiversity), the more functions are insured (functional diversity), and, since functions are related to ecosystem properties, the more stable an ecosystem is (stability). However, such a linear effect of biodiversity on ecosystem functioning is more and more controversial, and at least three alternative hypotheses were formulated for the relationship between biodiversity and ecosystem functioning (Díaz & Cabido 2001; Loreau *et al.* 2001; Scherer-Lorenzen 2005):

- the insurance hypothesis, according to which species functional niches are redundant and the loss of a species is compensated by another one (to some extent);
- the keystone species hypothesis, which states that some species make unique contribution to ecosystem processes and that their loss (or addition) causes detectable change in ecosystem’s functioning;
- the idiosyncratic response hypothesis, which says that species effects on ecosystem functioning are context-dependent (**Fig. I.3**).

All four hypotheses are defended by many scientists, but who generally focus on species richness, whereas most functional ecologists support the idea that ecosystem processes and properties are not driven by species richness but rather by functional diversity (Loreau 2000; Wardle *et al.* 2000; Díaz & Cabido 2001; Hooper *et al.* 2005; Petchey & Gaston 2006). These hypotheses should thus be assessed by quantifying functional diversity, measuring ecosystem functioning, and then investigating their relationship.

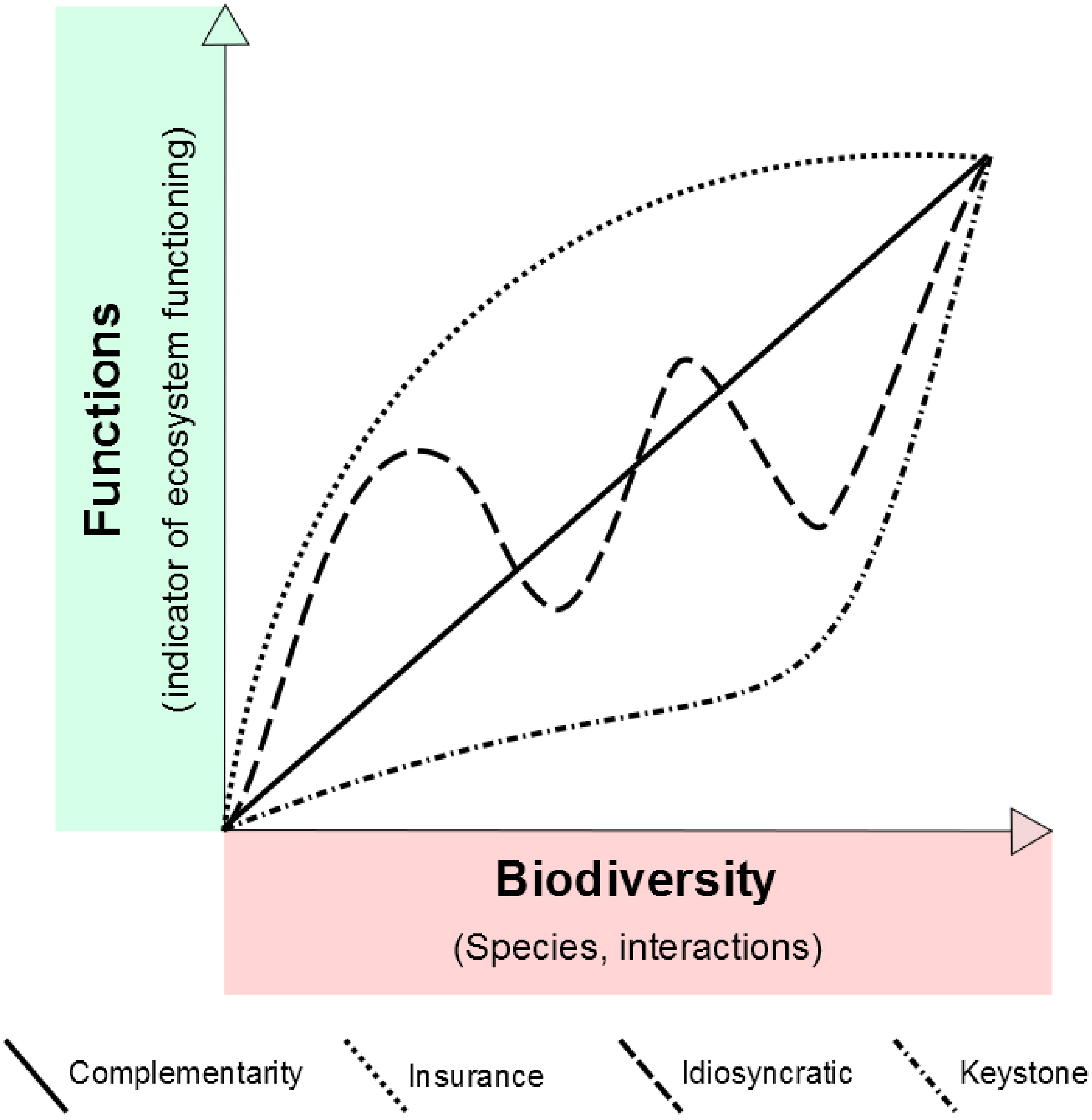


Figure I.3: Diagram illustrating the four alternative hypotheses about the relationship between biodiversity and ecosystem functioning (adapted from Naeem *et al.* 2002).

I.2 Approaches and scales of biodiversity

I.2.1 The trophic approach

An interesting way to link biodiversity to ecosystem functioning is to develop a trophic approach (Thompson *et al.* 2012). Since trophic networks (food webs) are maps of trophic interactions between individuals and species, they underlie one of the three main ecosystem processes, namely energy and biomass transfers across species. It is thus not surprising that a preferential way to estimate functional diversity is to measure functional traits related to resource use (e.g. trophic position, Díaz & Cabido 2001; Hooper *et al.* 2002; Petchey & Gaston 2006). Furthermore, trophic interactions, predator-prey relationships in particular, are considered as a main pathway for the propagation of perturbations in ecosystems and are thus directly concerned with ecosystem properties. It is indeed well recognized that disturbances can rapidly spread throughout trophic levels due to top-down or bottom-up trophic cascades, and thus impact many species that belong to the network (Duffy 2002; Montoya *et al.* 2006). For example, the loss of one particular species (a keystone species) or functional/trophic group may cause food web crash down. Trophic cascades (**Fig. I.4**) appear when species from successive trophic levels have strong trophic interactions and depend on each other. This phenomenon was already described in marine ecosystems, where top predators are disproportionately targeted by fishing, sometimes until extinction (Duffy 2002), implying cascading perturbations on species from lower trophic levels (Schmitz 2008; Baum & Worm 2009). One of the best illustration of top-down trophic cascade was described by Estes & Palmisano (1974) in the Pacific continental shelf ecosystem off the coasts of California, where sea otters indirectly allowed nearshore communities to develop in kelp beds by directly controlling sea urchins populations, the principal kelp feeder. When sea otters were missing, kelp beds and related communities were almost completely absent because the littoral area was carpeted with sea urchins.

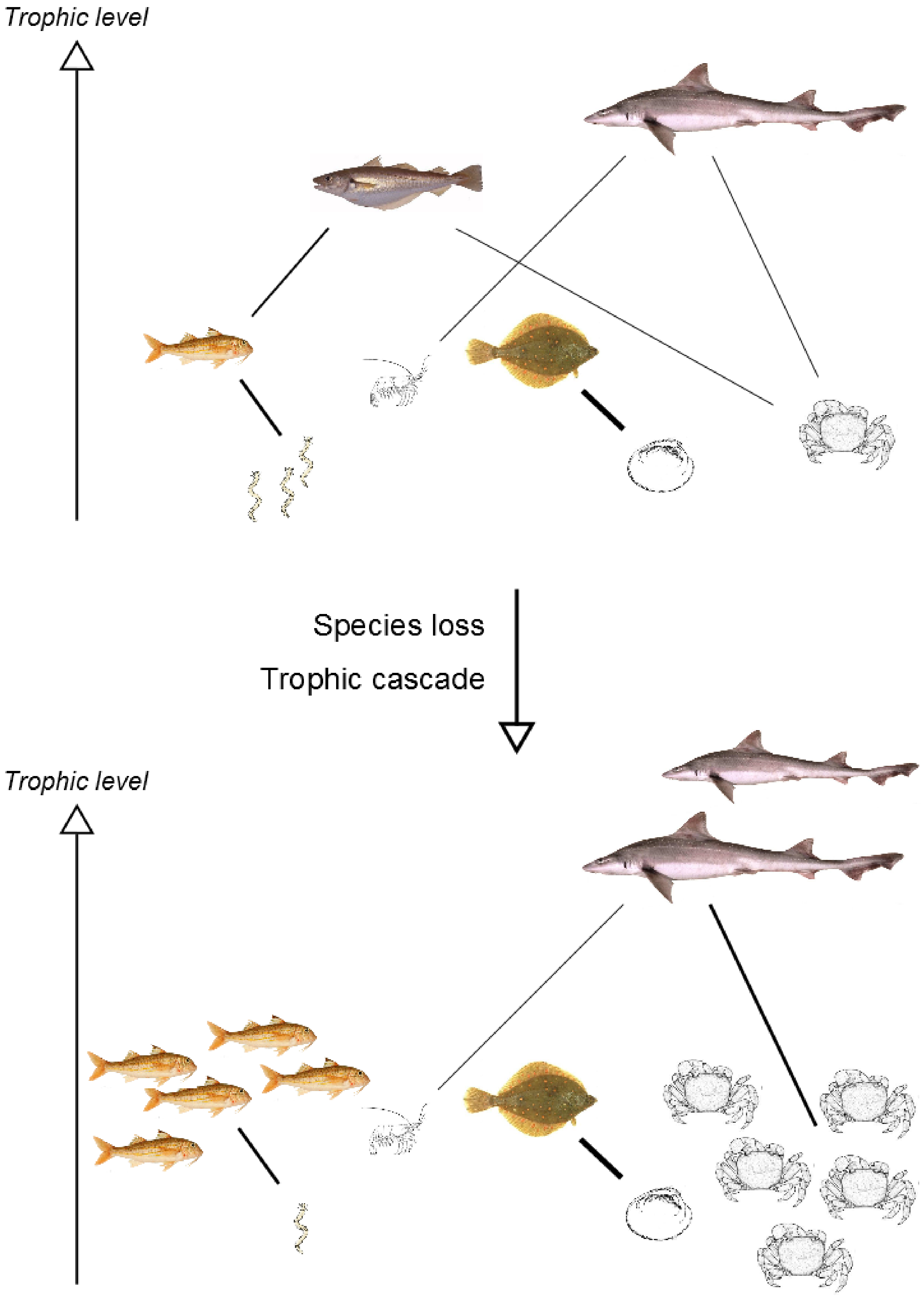


Figure I.4: A three-level trophic network illustrating that successions of strong trophic interactions can be main pathways for perturbation. Line width illustrates interaction strength.

Developing a trophic approach of communities and exploring the structure of associated trophic networks allow then to (i) classify species based on their food resource use (functional effect) and thus estimate functional diversity (**sections 1.4** and **1.6**, **Chap. III** and **V**), (ii) quantify the strength of the trophic interactions present in the food web (**section 1.4**, **Chap. III**), and (iii) hypothesize potential properties of the ecosystem (e.g. stability) based on the structure of its trophic network (**section 1.4**, **Chap. III**, Bengtsson 1998; Duffy 2002; van der Putten *et al.* 2004; Thompson *et al.* 2012). Measuring functional trait values of species and classifying them according to function was and still is a classical way to estimate functional diversity.

I.2.2 The morphological approach

Functional diversity does not, however, affect the process of energy and biomass transfer only and a species' function should not be restricted to its trophic role. The other two main ecological processes, namely geochemical cycles and other fluxes (e.g. water cycling), have to be taken into account and it is thus important to choose functional traits that are both measurable and related to several ecological functions. Throughout history, many scientists used morphology as a surrogate of organisms' ecology. There is indeed a long tradition of linking the shape of morphological features to ecological functions, which led to the development of the field of ecomorphology, originally based on Charles Darwin's observations on Galapagos finches (Darwin 1859). The key concept behind ecomorphology is that, since morphological shape integrates of evolutionary history, it is supposed to reflect adaptation to ecology, e.g. body shape adaptation to microhabitat utilization (Motta *et al.* 1995a), and many authors used morphology as a proxy for ecology notably in fish (Motta *et al.* 1995b; Norton *et al.* 1995; Albouy *et al.* 2011; Price *et al.* 2011; Farré *et al.* 2013). Furthermore, because the morphology of the whole body (or body shape) determines an organism's movements and locomotion (Wainwright 1991), it constrains the organism's interactions with its abiotic and biotic environment, and thus its ecological role. Therefore, an organism's body shape probably reflects several ecological functions and an integrative approach to assess functional diversity would be to use the diversity of organism body shapes. However, body shape, and thus probably ecological role or function, integrates not only adaptive evolutionary history but also phylogenetic history as body shape is one of the most fixed phenotypic character within lineages. It results that phylogenetic proximity between organisms may be reflected in morphological and/or functional proximity. A morphological approach to diversity based on body shape would thus allow to (i) consider several functional traits, and thus integrate several ecological functions of organisms at the same time (**sections 1.6** and **1.7**, **Chap. V** and **VI**); and (ii) estimate functional diversity through morphological diversity (**section 1.6**, **Chap. V**); but would also require to (iii) explore relationships between phylogenetic, morphological and functional diversity (**section 1.6, Chap. V**).

I.2.3 Considering individuals

During the last decade, more and more authors called for greater consideration of individual or intraspecific variability in community ecology in general, and in functional ecology in particular (Pachepsky *et al.* 2007; Bolnick *et al.* 2011; Albert *et al.* 2012). Functional diversity was originally defined as the “value and range of those species and organismal traits that influence ecosystem functioning” (Tilman 2001). The fact that not only the value but also the range of traits were taken into account in this definition indicates that assessing functional diversity necessitates individual-level measurements. Individual variation in functional traits around their species mean (variance) may have implication for ecological interactions and thus has to be considered for assessing functional diversity. According to Jensen’s Inequality, the average value $\overline{f(x)}$ of a non-linear function $f(x)$, representing for instance the strength of an ecological interaction involving individual with trait x, is different from the value $f(\overline{x})$ of the function evaluated at the trait mean $\bar{x}$. In ecological terms, Jensen’s Inequality says that, when ecological interactions do not depend linearly on an organism’s trait, the average interaction strength related to a trait, which characterizes the average ecological effect of a population or species, is not the interaction strength of the mean trait of individuals. Most importantly, populations differing in trait variation while having identical trait mean will be characterized by different average interaction strengths and thus ecological effects. Therefore, functional trait quantification needs to consider individual variation and to rely on measures at the individual level. Taking a trophic approach, individual variation in diet (or individual trophic niche variation) may alter the average competitive pressure between conspecifics or with individuals from other species and thus the population dynamics of predators, but also the average predation pressure and thus the population dynamics of prey, which together may ultimately have important implications for the trophic network structure and dynamics (Svanbäck & Bolnick 2008; Araùjo *et al.* 2011). More generally, individuals trait variation between species shapes biotic interactions and dynamics of the community (Bolnick *et al.* 2011). Within species, conspecifics differ in many ecological traits, and such individual niche variation promotes coexistence notably by relaxing competition within the population

(Bolnick *et al.* 2011). Ecological variation between conspecifics also implies individual variation in fitness, and thus is the main target of natural selection. Because of such eco-evolutionary consequences, it is essential to understand and clarify the patterns and causes of individual trait variation. For example, Van Valen (1965) described the "Niche Variation Hypothesis" (NVH) which states that wider ecological niches would permit greater phenotypic variation among conspecifics (pattern), and since then, individual niche variation were attributed to differences in size, age or gender, but also in intra- and inter-specific competitive pressures (causes). Focusing on a trophic approach (**section 1.5**, **Chap. IV**), patterns of individual diet variation between species can be investigated in relation to (i) species trophic niche breadth, since a broader species niche should permit larger individual diet variation (NVH), and (ii) species functional identity, since the function performed by a species may require a certain degree of ecological specialization that constrains the level of individual diet variation (and its trophic niche breadth). Within species, individual diet variation can be (iii) characterized in terms of the pattern of individual occupation of the species trophic niche and the degree of individual diet specialization, and (iv) its individual determinants, such as variation in individual state or habitat. Alternatively, since morphology is directly implicated in organism hunting modes, prey detection, and handling abilities, it is also supposed to somewhat constrain its prey consumption and thus its diet (Wainwright & Richard 1995; Ferry-Graham *et al.* 2002). So, based on the idea that an organism's morphology reflects its trophic ecology, related issues can be tackled through a morphological approach (**section 1.6**, **Chap. V**). More precisely, at the between species level, individual morphological variation can be related to (i) species trophic niche breadth to test for the Niche Variation Hypothesis, and (ii) to species functional identity to assess functional constraints on the level of variation. Finally, the association of individual morphological variation with (iii) individual diet variation, and by extension with variation of trophic relationships within the community, can be evaluated.

I.3 Objectives of the thesis

Based on the fish community of the eastern English Channel taken as a case study, this PhD thesis was motivated by the study of trophic organization within animal communities and its dependency on intra- and inter-specific morphological and functional traits variation. The eastern English Channel is a temperate continental shelf ecosystem exploited for decades. An assemblage of sixteen fish species was studied in this thesis (Teleosteii and Elasmobranchii). These species were chosen for their representativeness of the eastern English Channel fish community in terms of their abundance in the community and their commercial interest, but above all because they exhibit a wide diversity of ecological characteristics, and thus potentially a wide diversity of ecological functions.

A first step was to identify fish species trophic identity as well as trophic interaction strengths in order to establish the structure of the trophic network involving the fish community of the eastern English Channel (**Chap. III**). It allowed developing a trophic approach for exploring the functional diversity of the fish community and potentially relating it to ecosystem processes (**section 1.2.1**). A second step was still based on a trophic approach but considered individuals. It focused on the implication of individual diet variation, but also species trophic characteristics and functional identity, for the trophic organization of the fish community (**Chap. IV**). To this purpose, it tested for the Niche Variation Hypothesis (NVH; Van Valen, 1965) applied to species trophic niche within the community, and investigated its links with potential inter-specific competition (niche overlap) and species functional traits. A morphological approach was used in a third step, based on the hypothesis that morphology can be used as a surrogate for ecology. It sought to explore the link between phylogenetic, morphological and functional diversities across fish species of the assemblage, in order to clarify whether morphological or phylogenetic diversity are relevant indicators of functional diversity in natural community (**Chap. V**). Including individual level considerations, it also aimed to test for the Niche Variation Hypothesis applied to species trophic niches in combination with individual morphological variation within the community. The final step of this thesis was to identify the main determinants of trophic relationships at the individual level in the whole fish community. The contributions of phylogeny, morphology and individual state variation (endogenous factors) as well as habitat diversity (exogenous factor) to individual diet variation across species of the fish community were assessed and quantified (**Chap. VI**).

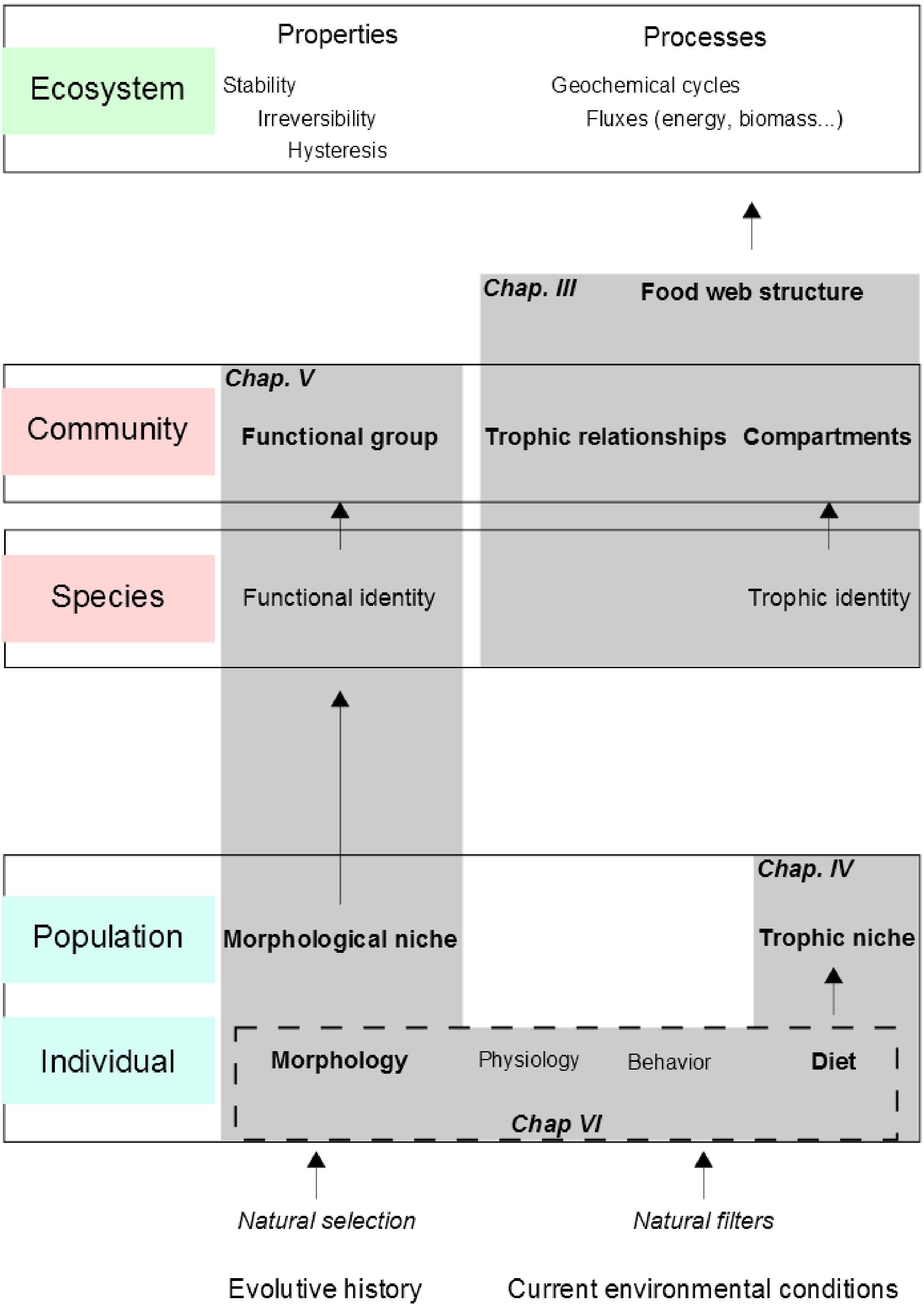


Figure I.5: Diagram of the organization of the PhD thesis.

I.4 Exploring trophic network structure

Glossary:

Trophic cascade: initially defined as the effect of predators on their prey and the indirect consequences on lower trophic levels, i.e. as top-down phenomena. Today, includes bottom-up cascades.

Trophic compartment: species or group of species related by strong trophic interactions and interacting weakly with other compartments.

Trophic identity: characterizes a species or a group of species by its set of predators and prey; in other words, species membership to a trophic compartment.

Original: characterizes a species or individual that uses a subset of available resources, which is not used by another species or individual.

The structure of a trophic network may be directly implicated in ecosystem stability, notably because of trophic cascades that may destabilize the whole ecosystem. It is thus crucial to understand how trophic network structure affects ecosystem functioning and stability (Sutherland *et al.* 2013). For this purpose, a first step is to determine the network structure itself, which necessitates establishing species trophic identity but also incorporating energy flow by estimating the strength of trophic interactions (Petchey & Gaston 2006; Rooney & McCann 2012). Then, a second step is to identify its determinants and finally to relate food web structure to ecosystem functioning (Thompson *et al.* 2012).

The trophic identity of a species (or of a group of species) is generally defined by its set of predators and prey. However, in empirical studies such as in **Chap. III**, it is often defined by prey items only due to the difficulty in sampling the whole trophic network and thus in obtaining a representative sample of the predators of a given species – inversely, a relatively good sampling of prey items of a given species is obtained by stomach content analysis. Trophic identity appears particularly important in the case of keystone species/group that may have a dominant effect on one or more trophic relationships, for example in the case of a predator that is the only one foraging on a particular prey in a community. Another example highlighting the importance of trophic identity is omnivory, a particular identity that is currently a matter of some debate. Usual models of food web indeed predict that omnivory is destabilizing communities, while empirical studies tend to conclude that omnivory has a stabilizing role on food webs by short-circuiting trophic cascades (Fagan 1997; Duffy 2002; Bascompte & Melian 2005). It is thus essential to identify the trophic identity of a species (or of a group of species) since it may be implicated in ecosystem functioning and is even sometimes directly related to stability (Harvey *et al.* 2012; Poisot *et al.* 2013).

In order to determine the structure of a trophic network, it is also important to estimate trophic interaction strength. It is intuitively obvious that the architecture of a network does not only depend on the diversity of species (or group of species) trophic identities, but is also shaped by the actual strength of interactions that relate these species (Strogatz 2001). Furthermore, during the last decade, studies of trophic interactions strength detected a common non-random pattern characterized by "few strong and many weak interactions" that reveals the general tendency for food web architecture to be compartmentalized, which tends to promote food web stability (Krause *et al.* 2003; Newman 2006; Belgrano *et al.* 2009). Food webs are thus generally composed of only a few strong trophic interactions, relying on trophic specialists (i.e. species feeding only on a subset of available prey items, and thus that highly depend on it) belonging to specialized compartments; and many weak interactions relating compartments and involving trophic generalists (i.e. species feeding on a wide diversity of prey, and that do not depend on a particular subset of prey items) that compose generalized compartments. Weak interactions tend to buffer variation of the food web structure (McCann *et al.* 1998; Bascompte *et al.* 2005; Rooney & McCann 2012), and since they, in part, rely on omnivorous species, it follows intuitively that omnivory stabilizes food web.

In **Chap. III**, trophic interaction strengths in the trophic network associated with the eastern English Channel fish community were estimated by the proportion of prey items found in species diets as determined by stomach content analysis. A compartmentalized network architecture was detected, including both generalized compartments that gathered generalist species (omnivorous), specialized compartments that included highly specialized species (e.g. planktivorous) and even an original species, plaice, that generated unique trophic interactions in the food web.

Chap. III also aimed at identifying the determinants of the food web architecture. Since fish species generally exhibit ontogenetic diet shift related to ontogenic habitat shift due to a change of ecological niche, including trophic niche, with life stage and more loosely size, it may be hypothesised that they also exhibit an ontogenetic functional shift (Polis 1984; Link 2002). Size was thus tested as a determinant of trophic interactions. In the same manner, since food web topology is influenced by involved taxa, spatial variation or even segregation of communities would imply that trophic networks are spatially variable (van der Putten *et al.* 2004; Thompson & Townsend 2005; Duffy *et al.* 2007; Thompson *et al.* 2012). Depth, used as a proxy for the nearshore-offshore gradient that occurs in continental shelf marine ecosystems such as the eastern English Channel, was therefore tested as another potential determinant of trophic interactions. Among these two potential determinants, size appeared to have a minor effect, except for one species that exhibited an ontogenetic diet shift, namely horse mackerel. It was revealed by the fact that individuals of this species changed trophic compartment, and thus trophic identity, as they grow, which supports the idea of an ontogenetic functional shift. It is worth noticing that the weakness of the size effect for most species may be related to the fact that all individuals in this study were at the juvenile or adult stage, whereas strong ontogenic shifts are mostly expected following metamorphosis from the larval to the juvenile stage. In contrast, depth was detected as a major factor implicated in trophic interactions, implying a spatial gradient in trophic relationships from the nearshore to the offshore area.

Network metrics were then computed to assess differences in the network architecture due to ontogeny and space. Network metrics were originally developed in the field of graph theory, but are now widely used to depict the architecture of food webs because it allows to identify trophic compartments and their composition (Newman 2006) as well as to compute metrics characterizing food web structure such as linkage density, the average number of trophic links per species, connectance, the proportion of actual trophic links relative to potential ones, or modularity, a measure of the degree of compartmentalization of the network (see Dunne 2012). These metrics give the opportunity to estimate but also to compare easily the architecture of food webs across ecosystems worldwide (Dunne *et al.* 2004). In **I. II**, network metrics allowed to highlight variation in the food web architecture related to depth (**Fig. I.6**), the food web at the scale of the eastern English Channel comprising two contrasted sub-networks along the coastal-offshore gradient, mainly differentiated according to the presence (offshore) or the absence (nearshore) of omnivorous species. In fact, mobile high-trophic-level species linked the two sub-networks in a meta-community structure, by moving from one community to the other to feed on different prey (McCann *et al.* 2005).

Chap. III conclusions were that (i) only one species underwent an ontogenetic functional shift, which highlighted the minor implication of size in the food web structure associated with juvenile and adult life stages; (ii) the structure of the eastern English Channel food web varied along the nearshore-offshore gradient revealing a meta-community structure composed of two sub-networks (one nearshore and one offshore) exhibiting contrasted architectures, (iii) the presence/absence of omnivorous species was responsible for the change in architecture between sub-networks, suggesting that the offshore sub-network was more stable as it included omnivorous species (**Fig. I.6**).

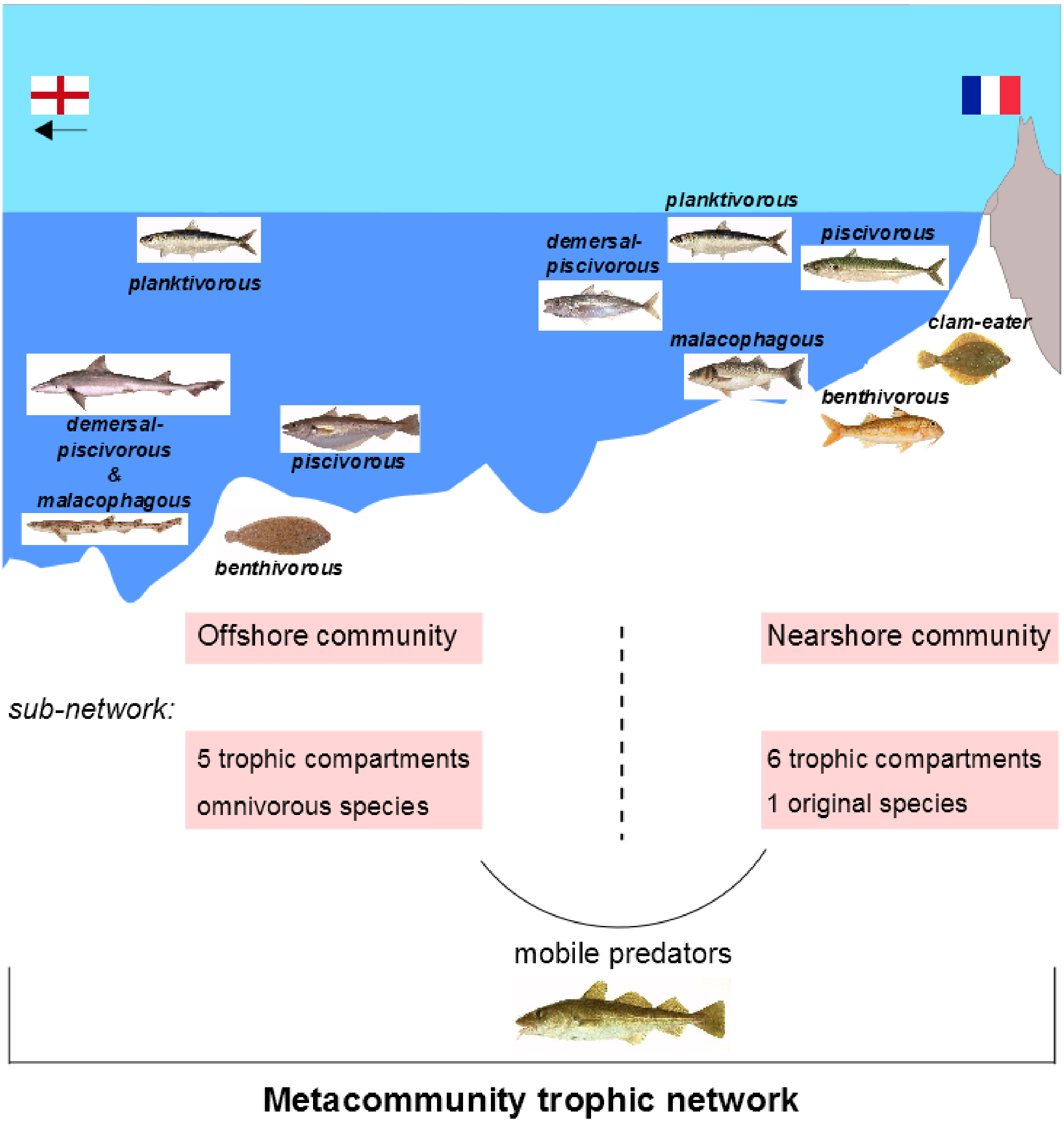


Figure I.6: Illustration of the principal results of **Chap. III** regarding the trophic network associated with the eastern English Channel fish community.

The hierarchically nested components of the architecture of the trophic network associated with the eastern English Channel fish community highlight the importance of considering three levels of organization in trophic ecology (Schoener 1989), and more generally in community ecology:

- metacommunity and community (trophic compartments),
- populations (trophic identity),
- individuals (individual variation due to size and/or habitat).

Traditionally, the individual level was however not considered of primary importance in the field of community ecology. Yet, at the very basis of community organization, particularly in trophic terms, are individuals that may differ, and their variation is increasingly recognized as having important effects on the structure and dynamics of food webs, communities and ecosystems besides those on population and evolutionary dynamics traditionally considered (Bolnick *et al.* 2011; Thompson *et al.* 2012). Empirical studies greatly support that individual variation is widespread (Bolnick *et al.* 2003) and the consequences of this variation for the concept of niche commonly used in community ecology can be represented through a simple mathematical model:

$$\boxed{TNW = WIC + BIC} \qquad (1)$$

where TNW is the total niche width of the population/species considered, WIC represents the individual niche width (Within-Individual Component), and BIC corresponds to niche variation between individuals (Between-Individual Component). Individual variation, particularly in the case of food resource use, may have important implications for both ecology and evolution. Ecologically speaking, more variable populations are expected to be more stable facing competition or predation, to maintain different selective pressures on prey, and to diversify faster, which in turn affects population and community processes and dynamics (Bolnick *et al.* 2003, 2011; Araùjo *et al.* 2011). Evolutionarily speaking, individual variation implies that individuals may have different fitness values, and thus may be subject to different selective pressures, sometimes leading to adaptive radiation, e.g. Darwin finches (Price 1987; Bolnick *et al.* 2003).

I.5 Individual trophic niche variation

Glossary

Generalist: species or individual that uses the whole set (or most) of available resources.
Specialist: species or individual that uses only a subset of available resources.
Functional group: group of species or individuals sharing the same ecological function; often determined on the basis of functional trait value proximity.
Functional identity: characterizes an organism by its set of functional trait values; in other words, organism membership to a functional group

Variation between individuals was already studied in many papers for its implications in ecology and evolution, but its importance for population, community, and ecosystem dynamics remains a major issue in science (Sutherland *et al.* 2013). A specific theory, the Niche Variation Hypothesis (NVH, Van Valen 1965), addresses the relationship between individual variation and species ecological niche. The NVH indeed states that a wide population ecological niche would permit greater variation among individuals than a narrow one, which in terms of equation (1) means that the larger TNW, the larger BIC can be. Since the realized ecological niche (be it at the population/species or individual level) is intended to result from environmental conditions but also biotic interactions, the NVH would imply that observed population and individual niches are, at least partly, determined by biotic interactions such as competition. It is thus essential to go further than testing the NVH by identifying the mechanisms generating individual niche variation, whether it be processes related to individual state (e.g. ontogenetic niche shift) or competitive pressures (Bolnick *et al.* 2003). Another important aspect is that the NVH was originally formulated, and since then empirically tested (Galeotti & Rubolini 2004; Meiri *et al.* 2005; Hsu *et al.* 2013) with respect to variation of niche width across populations of the same species (or across close species from the same taxon) in different ecosystems. However, niche breadth varies also across species within a given community and the NVH could apply along this axis of variation. Although it would have important implications for niche partitioning and assembly, this possibility was never tested empirically.

Expressed in trophic terms, a species with a large trophic niche, i.e. a generalist species that uses a wide diversity of prey items, may actually be composed of either generalist individuals, i.e. using the same resources as their species-as-a-whole, or different specialist individuals, i.e. using different subsets of resources used by their species-a-whole (Bolnick *et al.* 2007). In terms of equation (1), this means that the larger TNW, the larger BIC but also WIC can be and thus that the NVH is not to be taken for granted. However, results of **Chap. IV** support the Niche Variation Hypothesis applied across fish species from different trophic levels and habitats in the eastern English Channel community. More precisely, a positive correlation was detected between species trophic niche breadth and individual diet variation based on stomach content data.

Besides testing the NVH, it is important to focus on the processes responsible for niche variation. Whether it be across or within species, trophic niche variation is expected to result from competition for food resources. Strong inter-specific competition is indeed expected to cause species niche diversification (competitive diversification), notably by character displacement, and individual niche convergence in order to mitigate interactions with individuals from other species, leading to a contraction of the species niche and a decrease in individual niche variation (Araùjo *et al.* 2011). In contrast, when released from inter-specific competition, individuals experiencing strong intra-specific competition are expected to diversify their niches, implying an increase in individual niche variation and an expansion of the species niche (Svanbäck & Bolnick 2007; Bolnick *et al.* 2010). However, the organization of species and individual niches are not only depending on current biotic interactions, but also on their evolutionary history that may be related to past competitive pressures. A long history of inter-specific competition may lead to character displacement and adaptive radiation, whereas the resulting niche partitioning suggests the absence of current inter-specific competition (Schluter 1996, 2000). In the same manner, species may undergo convergent evolution towards using the same resources when those are abundant enough such that they are not limiting and do not generate competition, whereas the resulting overlap between niches suggests strong current inter-specific competition. In **Chap. IV**, trophic niche overlap between fish species of the eastern English Channel was used as an estimation of inter-specific competitive pressure, but failed to be correlated with species trophic niche breadth and individual diet variation. It was thus hypothesised that (i) some food resources in the eastern English Channel are abundant enough to sustain the fish community without any limiting effect such that (ii) species may have evolutionarily converged towards using the same abundant food resources.

As introduced in **section 1.2.3**, from a functional perspective, niche variation may be linked to the ecological functions performed by species. Following the idea that some functions necessitate a certain specialization of species and thus of their ecological niche, probably resulting in weak individual niche variation a new approach to the NVH was tested. If there is indeed a gradient of species niche breadth/individual niche variation, it may be possible that functional specialists are positioned at the narrow species niche/low individual variation extreme, whereas functional generalists, i.e. species assuming functions that do not require for specialization, would be positioned at the other extreme, i.e. broad species niche/large individual variation. In **Chap. IV,** several functional traits related to species usual habitat and foraging strategy were used to assess species functional identity. It was defined as species membership to functional groups determined by clustering of the matrix of species functional trait values. Correlations expected from the NVH (niche breadth-individual variation, niche overlap-niche breadth, niche overlap-individual variation; *see above*) were then investigated within and across functional groups instead of across species as previously. Unfortunately, correlations across functional groups were not significant, probably because of a lack of statistical power linked to the low number of functional groups (5 only). However, their values were extremely close to those found in across species, suggesting that functional groups are distributed along the species niche breadth/individual variation gradient and that functional identity may partly constrain species niche. Correlations within functional groups were themselves significant and also close to those observed across species, suggesting that taxonomic identity within functional groups also matters. The NVH was therefore supported at various levels of organization, although the lack of significances across functional groups calls for additional studies involving more functional groups.

The NVH being successfully supported across species, **Chap. IV** investigated patterns of individual variation within species, focusing on the individual occupation of the species niche. Individual occupation may take several patterns for species with large niche breadth (generalist species). As already described above, a large niche breadth can be occupied by (i) specialist individuals or (ii) generalist individuals, but it can also rely on (iii) a combination of generalist and specialist individuals, or (iv) several specialized groups of individuals (Bolnick *et al.* 2003; Svanbäck & Persson 2004; Svanbäck & Bolnick 2005; Araùjo *et al.* 2008, 2010, 2011; Svanbäck *et al.* 2011). In terms of equation (1), this means that the larger TNW, the larger BIC (i) or WIC (ii) can be or both at the same time (iii and iv). Given that the NVH was successfully supported, option (ii) can be eliminated but the other ones are still possible. Using metrics of individual-level networks describing similarity between individuals' diet composition within each species (see Araùjo *et al.* 2008), it was shown in **Chap. IV** that generalist species within the eastern English Channel fish community could exhibit the three potential patterns of individual variation expected from the NVH, namely all individuals being specialists (i), a combination of generalist and specialist individuals (iii), or several clusters of specialized individuals (iv). This result confirms that the studied fish community follows the NVH, according to which a large species niche allows individual diversification, and invalidates the parallel release theory, which states that a large species niche may result from or in a simultaneous increase in individual niche. All specialized species in the community were composed of similar individuals gathered in a single cluster with few outlier individuals.

Once patterns of individual diet variation within species are identified, the causes of this variability can be investigated. Individual diet variability is expected to result mainly from (i) phenotypic variation between individuals for instance in terms of behaviour, physiological requirements (that may be related to life stage, sex, etc.), social status, foraging experience, and/or morphology (Bolnick *et al.* 2003, 2011; Svanbäck & Bolnick 2008; Araùjo *et al.* 2011), and/or (ii) variation in prey availability and abundance across different habitats. Implications of phenotypic and habitat variation in individual diet variability were tested in **Chap. IV**. Linear models were used to assess differences in maturity stage, sex, and size for phenotype and in depth as a proxy for habitat between individuals belonging to different clusters in generalist species exhibiting occupation pattern (iv) or between clustered and outlier individuals in specialist species. Only depth, sex and size varied between groups of individuals for a few species suggesting that the potential causes of individual variation tested had only a marginal effect, if any, on individual trophic niche variation for the studied fish species.

Chap. IV main conclusions were that (i) the NVH was supported across species trophic niches from different trophic levels within a community but without being able to relate it to competition; (ii) the NVH was supported within functional groups and potentially across functional groups despite non significance, suggesting that niche characteristics may be related to functional identity, an hypothesis that necessitates additional studies to be confirmed; (iii) since size, sex and habitat variation had only a marginal effect on individual trophic niche variation, other potential determinants of trophic interactions, such as morphology or behaviour, should be investigated (**Fig. I.7**).

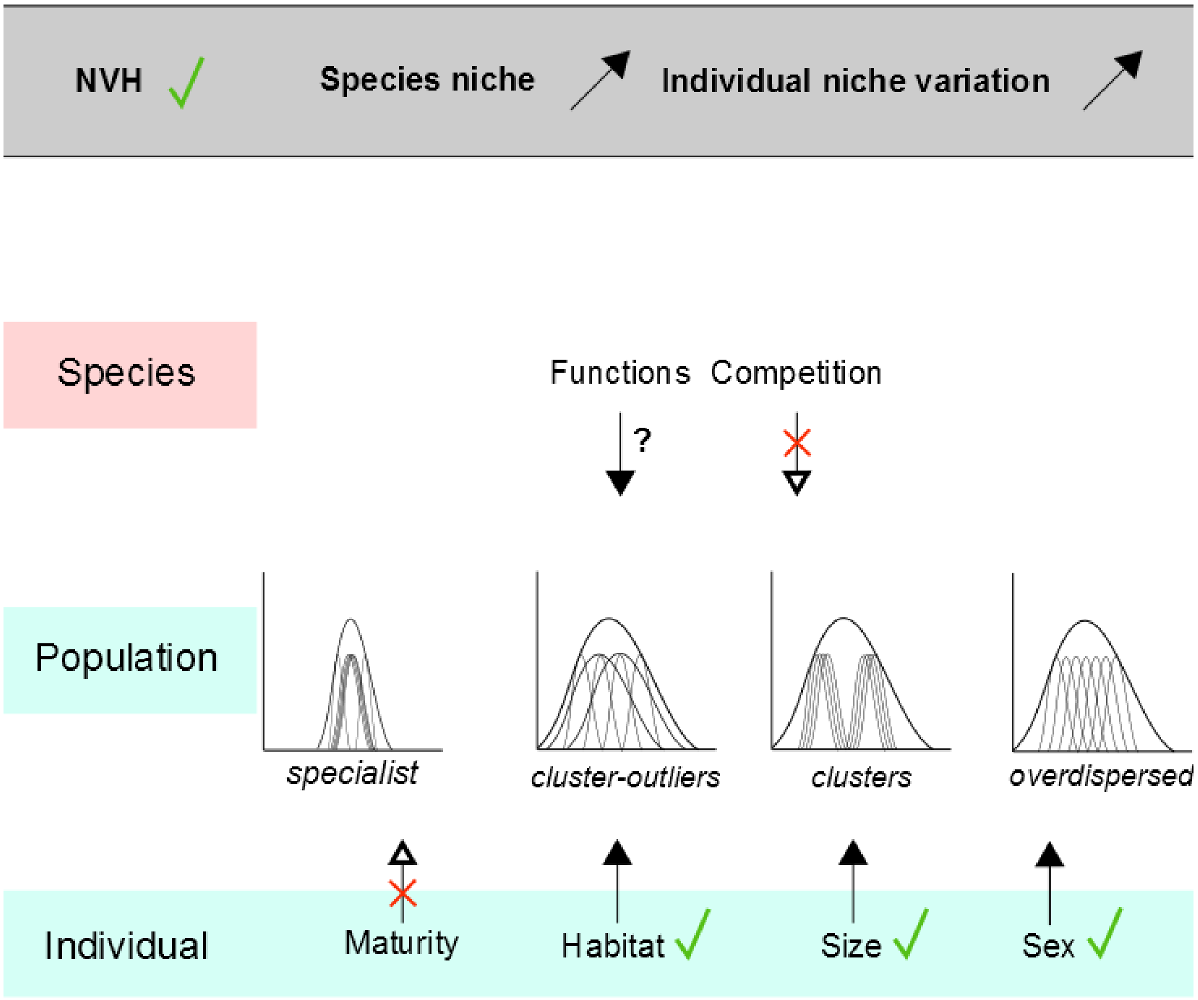
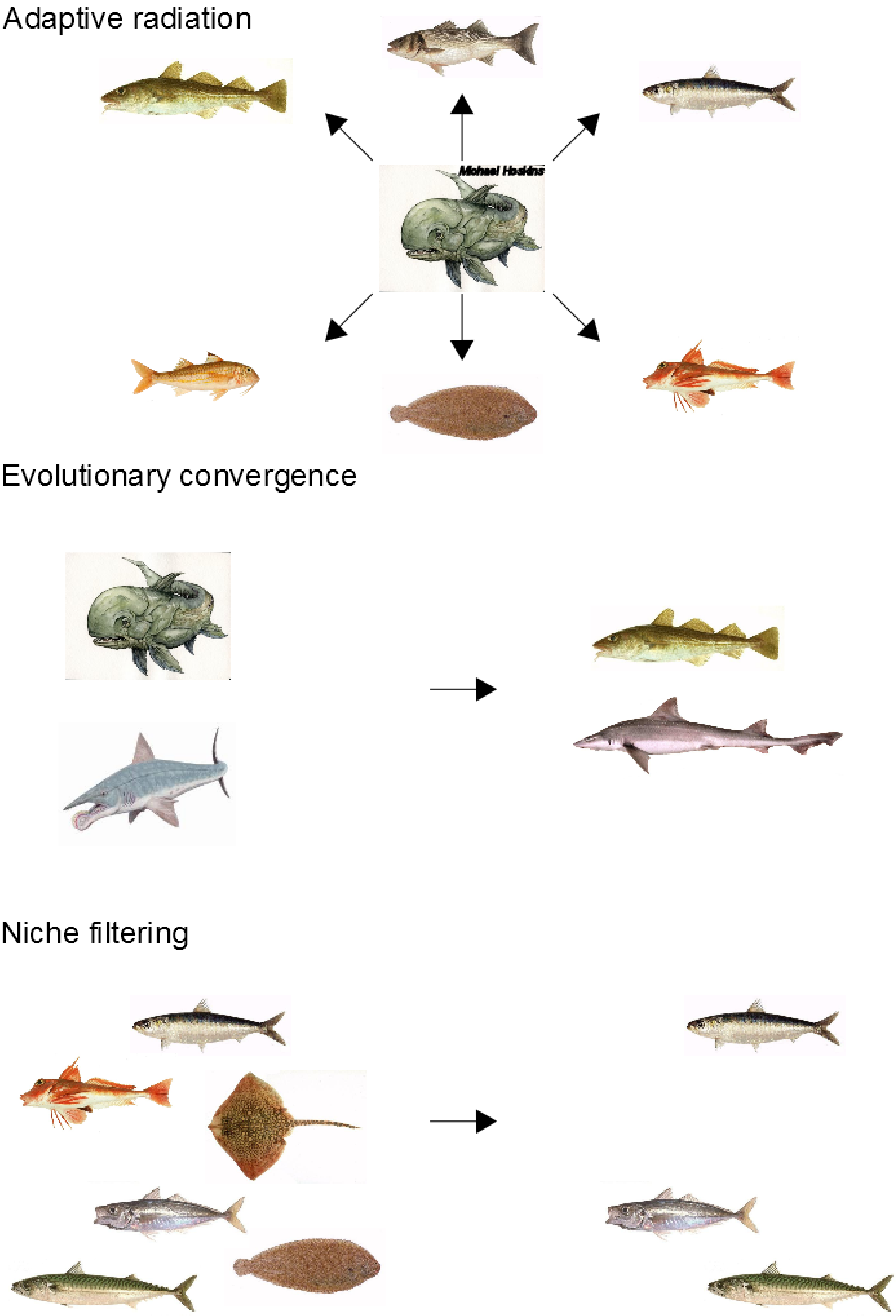


Figure I.7: Illustration of the principal results of **Chap. IV** regarding the Niche Variation Hypothesis within a community, adapted from Bolnick *et al.* 2003, 2011; Svanbäck & Bolnick 2008.

Results obtained through the trophic approach (**this section** and **section 1.4**, **Chap. III and IV**) highlighted the importance of diversity and niche variation in food web structure and community organization. Trophic traits, i.e. traits related to food resource use, are often employed in functional studies because, besides the fact that they are implicated in a major process of ecosystem (energetic and biomass transfers), they are measurable and their effects or consequences are relatively intuitive (e.g. trophic cascades). Choosing appropriate traits to estimate functional diversity is a main difficulty in functional ecology. Functional traits are expected to be measurable (either qualitatively or quantitatively) and, of course, informative about a particular function performed by the organism (Petchey & Gaston 2006). Such knowledge about trait(s) related to function(s) is challenging to acquire in natural community, particularly in marine environment where direct observations of organism are difficult and scarce. To circumvent this issue, it is possible to use traits that related to the ecology of organisms in general, and thus integrating several functions. Following this line, it appears necessary to relate, at least qualitatively, a measurable trait to several functions, even if the direct causation between the two is not quantifiable. As introduced in **section 1.2.2**, morphology has been related to organism ecology (ecomorphology) for a long time and it appears intuitive that an organism's morphology is implicated in several of its ecological functions. Since many authors assume that morphology is a relevant surrogate for ecology (Ricklefs & Travis 1980; Motta *et al.* 1995; Norton *et al.* 1995; Ricklefs 2012), it may be hypothesized that morphological diversity may be an indicator of functional diversity.

I.6 Phylogeny, morphology and functions

Estimating functional diversity by morphological diversity implies that drivers of the latter are also drivers of the former. The current diversity of niches or traits (functional or morphological) in natural communities is usually explained by two different aspects: how trait variation between species is originally generated and how existing trait variation between is assembled in communities. The origins of trait variation between species are most often explained by classic coexistence theory from evolutionary biology. Two main evolutionary processes will generate trait variation between species *via* character displacement. Adaptive radiation is the phenomenon of species trait diversification through evolutionary time until reaching coexistence equilibrium resulting from competitive exclusion (Schluter 1996, 2000). In contrast, evolutionary convergence corresponds to species evolution towards similar trait values as a response to similar selective pressures imposed by the environment. The way existing trait variation between species from a regional pool is assembled at the local scale is then generally explained by two community assembly rules that rely on direct ecological processes as opposed to evolutionary ones. Limiting similarity states that, according to competitive exclusion, species with dissimilar and thus complementary trait values will be assembled at local scale so as to limit the magnitude of competition. In contrast, environmental filtering is a process where environmental conditions act like a filter on specie, allowing only species with relatively similar traits values to coexist (**Fig. I.8,** Zobel 1997; Mouillot *et al.* 2007; Cadotte *et al.* 2013). Consequently, drivers of morphological and functional diversity may be evolutionary (adaptive diversification, evolutionary convergence) and/or ecological (limiting similarity, niche filtering) and may favour trait divergence (adaptive diversification, limiting similarity,) or convergence (evolutionary convergence, environmental filtering). When trait variation originates from adaptive radiation, traits are phylogenetically conserved, whereas in case of evolutionary convergence, they are not. Depending on the evolutionary origin of trait variation, trait and phylogenetic diversity might thus be related or not (Webb *et al.* 2002) and the observation of the relationship, if any, might be biased by the ecological processes governing community assembly at the local scale (Srivastava *et al.* 2012). In the same way as morphology can be related to ecological functions, phylogeny may thus be involved in the morphological and functional structure of communities, and the actual relationship between phylogenetic, morphological and functional diversity may help to identify the drivers of diversity.


Adaptive radiation

Evolutionary convergence

Niche filtering

Figure I.8: Illustration of the main community assembly rules.

Chap. V focused on the whole body shape and hypothesised that it is a compromise among most of the functions performed by individuals, without any *a priori* relationship between a specific morphological feature and a particular ecological function (Norton *et al.* 1995). Body shape has a strong genetic basis, suggesting that body morphology variation across species has a strong phylogenetic component. Given the assumption that body morphology reflects functional aspect of organisms, that would mean that phylogenetic diversity is related to functional diversity (Srivastava *et al.* 2012). At the same time, morphology is well known as a particularly plastic trait (West-Eberhard 1989), implying that a non negligible part of morphology is independent from genes. Therefore, assuming that body morphology is a surrogate for functional ecology, one issue is to determine to what extent morphology, and thus functional ecology, is phylogenetically conserved. In a functional ecomorphological approach, there is no escape but to deal with the question about phylogenetic *versus* functional diversity (Devictor *et al.* 2010).

Chap. V compared phylogenetic, morphological and functional diversity between 11 round fish species of the eastern English Channel community based on the hypothesis that phylogeny is somehow linked to functions through morphology. To reach this goal, a phylogenetic tree, a morphological tree and a functional tree were computed and compared. Mitochondrial cytochrome-*b* DNA sequences were used for producing the phylogenetic tree using maximum likelihood methods. 9 functional traits, that were intentionally not only related to trophic ecology but also to species usual habitat and swimming mode, were collected to compute the functional tree by hierarchical clustering. Body morphology of fish species was described using methods of geometric morphometrics. Twenty two homologous landmarks along the whole body were captured on numerical pictures of each individual of each species and superimposed using Generalized Procrustes Analysis. The resulting morphological data, so-called Procrustes residuals, were used to compute the average configuration of landmarks for each species (mean individual morphology), the coordinates of which were used to compute the morphological tree of the assemblage by hierarchical clustering. It appeared that the topology of the phylogenetic tree did not match that of the morphological and the functional tree. In addition, phylogenetic distance (extracted from the phylogenetic tree) did not relate significantly to morphological variation across species although it explained roughly 29% of variance. In contrast, the morphological and the functional tree matched perfectly, and the affiliation of species to a functional group significantly explained 28% of morphological variation.

Because morphological and functional diversity across species appeared related, it was decided to investigate the potential link morphology/function at the individual level by testing hypotheses derived from the NVH in a morphological approach and relate it to functional identity, as was done previously using a trophic approach (cf **1.5. Individual trophic niche variation**). It was again hypothesized that some functions may imply high morphological specialization, and thus a narrow species niche related to weak individual variation. Contrary to **Chap. IV**, results of **Chap. V** failed to support the NVH: no link between species morphological niche specialization, species trophic niche breadth, and individual morphological variation was observed, since no correlation was significant. In line with **Chap. IV**, no significant relationship between functional identity and (trophic) niche breadth and individual (morphological) variation was significant, potentially again because of a lack of statistical power due to the low number of functional groups (4 in this case).

Chap. V revealed (i) the perfect correspondence between morphological and functional diversity, (ii) the absence of relationship between phylogenetic diversity and both morphological and functional diversity (**Fig. I.9**). These results support the idea that phylogenetic diversity is not a relevant proxy for functional diversity in the community studied, but rather that morphological diversity is. More generally, it confirms the idea that morphology would be of better relevance than phylogeny for the field of functional ecology as the link between morphology and function should not be distorted by evolutionary and ecological drivers of diversity as the link between phylogeny and function might be (see *first paragraph of this section*). Using species from the same community but living in habitat of varying heterogeneity also allowed to infer that the functional composition of communities and the resulting functional and/or niche diversity depends on environmental heterogeneity, and that the taxonomic composition of functional groups is driven by niche filtering in common environmental conditions or common habitat (see **Chap. V** for more details). Finally, despite the link between morphological and functional diversity across species, **Chap. V** concluded on the absence of link between trophic niche breadth and individual morphological variation suggesting a discrepancy between the species and the individual level. This may be attributed to fact that fish are functionally versatile enough to assume similar trophic functions with dissimilar morphology, and/or dissimilar trophic functions with similar morphology.

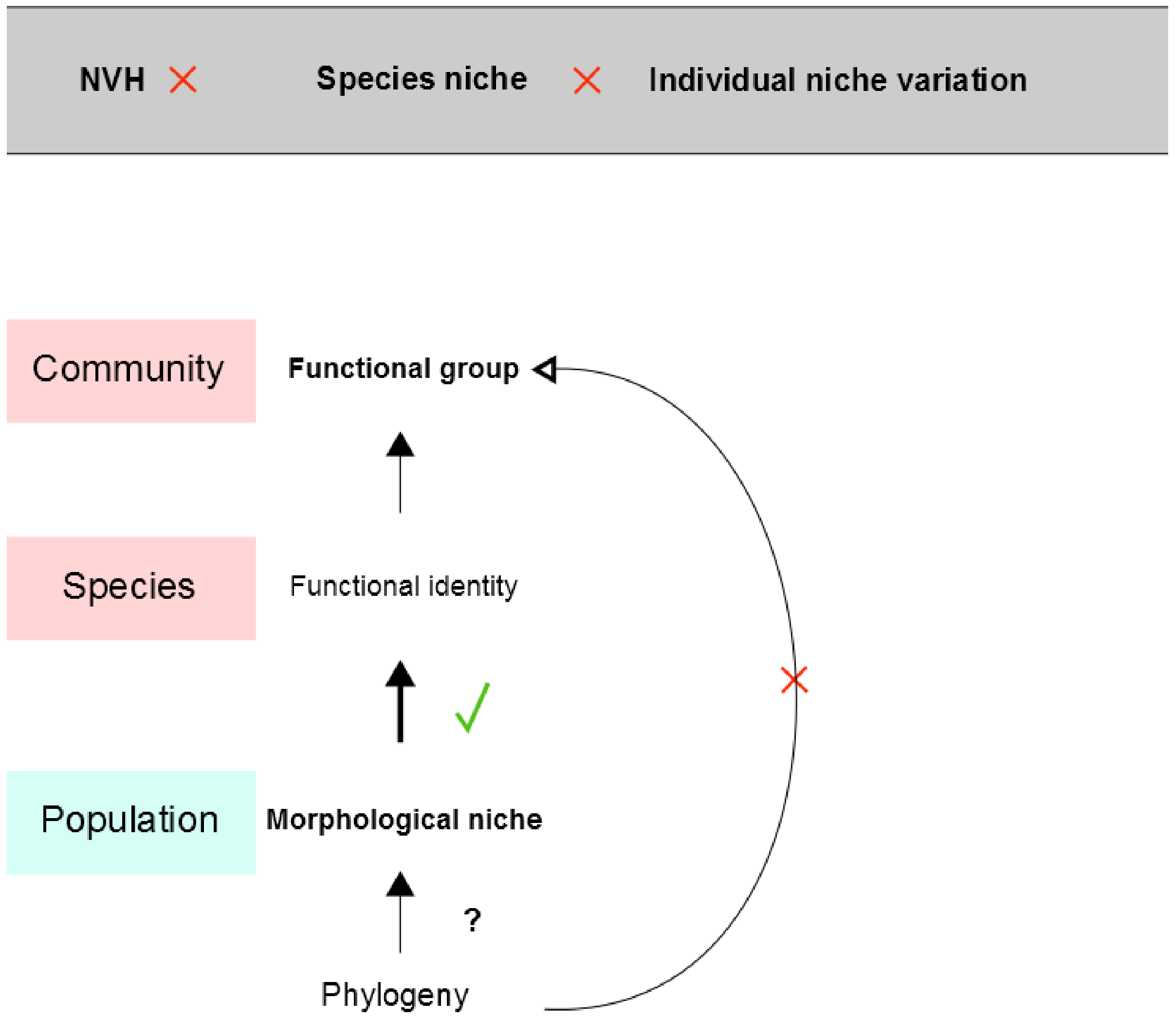


Figure I.9: Illustration of principal results from **Chap. V** regarding the relationship between phylogenetic, morphological and functional diversity.

Along the previous sections, it was firstly demonstrated that the trophic identity of species, as well as trophic interaction strengths were crucial for food web architecture (**section 1.4**, **Chap III**), but also that individual diversity within species will affect the trophic organisation of communities (**section 1.5**, **Chap IV**). Developing a morphological approach in a second step, it was shown that morphology was as a main factor implicated in species functional identity but that this link between morphology and function was maybe not supported at the individual level (**this section**, **Chap V**). These results motivate to focus in a next step on an individual-level approach to trophic function and evaluate its relationship with morphology in order to assess whether morphology is a determinant of trophic identity and interactions strengths, and ultimately to hypothesise about its implications for marine food web structure and ecosystem functioning.

I.7 Determinism of trophic interactions

I.7.1 Relationships between morphology and trophic ecology at the species level.

The link between morphology and trophic ecology has been the subject of a historical debate. On the one hand, some authors failed to find any (or significant) relationships between morphology and diet (Douglas & Matthews 1992; Labropoulou & Markakis 1998; Bolnick & Paull 2009), to the extent that this apparent mismatch between body shape and diet became a principle known as Liem's paradox (Liem 1980). Liem was studying fish and was surprised to observe that morphological specialists actually act as trophic generalists. As a reason, he suggested that fish have a strong tendency to exhibit feeding versatility, i.e. the ability to feed on a wide diversity of prey items linked for instance to environmental conditions. Two other explanations were given for the absence of correlation between morphological and trophic specialization, and both are based on competition and competitive exclusion. The first one, known as the competitive refugium theory, states that a morphological specialist uses available prey items when they are abundant, but switch to a specialized diet when resources become scarce in order to relax competition. The second explanation states exactly the opposite, i.e. that when resources are abundant, morphological specialists focus on their own prey, whereas when resources become scarce, they are forced to feed on remaining prey items and so that their diet and morphology mismatch (Robinson & Wilson 1998). In the fish assemblage of the eastern English Channel, food resources did not seem to be limiting (**Chap. IV**). The following section explore whether there is a mismatch between morphological and dietary specialization at the species level in the eastern English Channel fish community.

I.7.2 Testing for Liem's paradox

A species' morphological specialization was assessed by the distance *MD* between the centroid of its morphological niche to the centroid of the assemblage, considering that the more distant is a species' niche from the centroid of the morphospace, the more specialized is the species' morphology (Bellwood *et al.* 2006). The morphospace comprised 16 fish species chosen as the most representative ones of the eastern English Channel fish community and was determined by Generalized Procrustes Analysis on the (semi-)landmarks describing individuals body shape (see **section 1.6** and **Chap. V** for more details). Then, following Feinsinger *et al.* (1981), a diet specialization index was estimated for each of the 16 species as the proportional similarity index PS_j between species j's diet expressed in terms of proportions of the different prey classes and the proportion of the different prey classes in all-species' diet (see **Chap. III** for more details) .

First, species were represented in the assemblage morphospace according to their mean morphology (average landmark configuration) and were attached a symbol corresponding to their level of dietary specialization PS_j (**Fig. I.10**). Only the first two axes of the morphospace were represented as they account for 88.8 % of morphological variance in the assemblage (axis 1 = 52.3% and axis 2 = 36.5%, **Fig. I.10**).

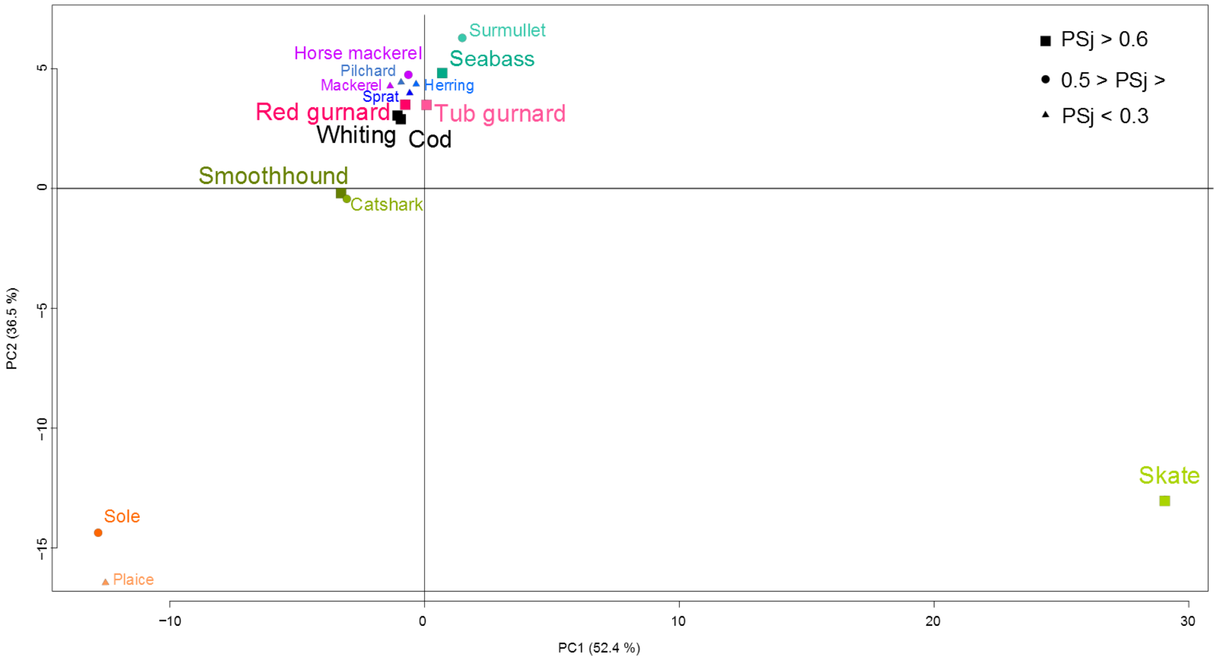


Figure I.10: Representation of the morphological position of species in the assemblage morphospace with symbols corresponding to their level of dietary specialization (PS_j).

No clear relationship appeared between species morphology and their degree of diet specialization **(Fig. I.10)**. A Spearman correlation test between the index of morphological specialization and dietary specialization confirmed this result as it was non significant (P-value = 0.83; correlation coefficient = 0.06). Our results clearly reveal a mismatch between species morphological and diet specialization in the eastern English Channel fish assemblage. To our best knowledge, this is only the second time that evidence for the existence of Liem's paradox is found in a marine community, the first one being on coral reef (Bellwood *et al.* 2006). This result however holds at the species level and thus does not totally preclude the existence of a link between trophic and morphological ecology. Specifically, part of the debate about the link between morphology and diet came from the fact that some other authors detected a clear (but weak) link (Wainwright & Richard 1995; Wainwright 1996; Wainwright & Bellwood 2002; Svanbäck & Eklöv 2003; Ibañez *et al.* 2007). This result is more in line with intuitive expectation since, as already mentioned, morphology is supposed to constrain an organism's movements and locomotion, and thus to be involved in its swimming and hunting modes, prey detection capability, handling ability, etc. (Wainwright & Richard 1995; Ferry-Graham *et al.* 2002). One way to make progress the debate would be to develop an individual-based approach.

I.7.3 On the implication of phylogeny, morphology, habitat and individual state on trophic relationships in a marine fish community

Being able to relate morphology and trophic ecology would be invaluable for predicting trophic interaction strengths, food web structure, and maybe ecosystem responses to perturbation (e.g. trophic cascades, Sutherland *et al.* 2013). It would also be an important step forward for ecology if morphological traits were relevant tools to predict ecological network structure, as they are easy to measure and in a non-intrusive manner (prediction of ecology of endangered species based on pictures for example) Applications would probably touch on many ecological domains, such as conservation, naturalism, or the link between ecology and paleontology (morphology is almost the only measurable characteristic in fossils). However, other factors than morphology may influence individuals' diet and it is of main importance to test all potential determinants of trophic relationships and to quantify their respective contribution to diet variation. To reach this goal, it is necessary to use an individual-level approach with individuals belonging to different species characterized by varying trophic levels and contrasted ecological functions.

Developing an individual-based approach is justified by the fact that individual diet variation has several consequences. Firstly, diet is essential for energy acquisition and thus of primary importance for an individual's fitness (Svanbäck & Bolnick 2008). Consequently, individual diet variation may be directly implicated in species evolution as natural selection acts on fitness differentials. Secondly, diet is involved in major biotic interactions in communities, i.e. competition, facilitation and/or predation, whether it be with conspecifics or individuals from other species. Therefore, individual diet variation directly shapes food web structure, and thus affects energy and biomass transfer in ecosystems and their properties. In a nutshell, individual diet variation is a target of natural selection and influences ecosystem functioning.

It is thus not surprising that one issue in evolutionary and ecology research is to identify the determinants of individual diet variation (Svanbäck & Bolnick 2008). The principal theory that addresses the determinants of individual diet variation is Optimal Foraging Theory (OFT, Schoener 1971; Werner & Hall 1974). OFT states that an individual forages on a given prey item in order to maximize its benefits, such as energy intake, against costs, such as foraging and handling time, to digestion energetic costs or exposition to predators. OFT identifies two main categories of potential factors implicated in the determination of foraging strategy: those related to resources (prey availability, energetic value, defensive traits) and those linked to the forager itself (morphology, behaviour and/or physiological needs; Svanbäck & Bolnick 2008; Dall *et al.* 2012). It is intuitive that the first filter of the consumption of a prey is its encounter, and that prey availability and abundance are of course some of the main factors that may explain individual diet variation (Ferry-Graham *et al.* 2002). Then, consumer's foraging ability and feeding requirements come into play. A consumer needs to be able to detect, recognize, attack and consume the prey (Ferry-Graham *et al.* 2002). Foraging ability but also feeding requirements may vary between conspecifics according to size or age due to ontogenic diet shift, sex due to sexual dimorphism, morphology, and/or behaviour related to social status, preferences or experience. Since variation in individual behaviour is hard to measure, particularly in marine organisms, morphology and individual state (characterized by traits such as size, age, life-stage etc.) were the main potential determinants of food resource use studied. However, as explained in **section 1.6** and **Chap. V**, morphology is expected to have a strong genetic component, and more particularly to be phylogenetically conserved. Behaviour may also be partly genetically coded (Krebs & Davies 1991) and be phylogenetically conserved. As a consequence, understanding the determinism of individual diet variation requires to estimate the direct and indirect contributions of four main factors: (i) prey availability, (ii) phylogeny, (iii) morphology, (iv) individual state characterized by e.g. size, sex, or physiology.

Chap. VI aimed at partitioning individual diet variation according to these four factors in the same assemblage of 16 fish species from the eastern English Channel as the one used to test Liem's paradox (**sub-section 1.7.2**). Habitat and prey availability were represented by the composition of the demersal community of invertebrates and vertebrates at the location of capture of individuals. Phylogeny was accounted for using the most relevant Principal Components of the matrix of phylogenetic distances between species that was extracted from a phylogenetical tree based on mitochondrial cytochrome-*b* DNA sequences (see **section 1.6** and **Chap. V** and **VI** for more details). Morphology was described by the matrix of Procrustes residuals that was obtained after Generalized Procrustes Analysis on twenty two homologous landmarks describing the body shape of each individual (see **section 1.6** and C**hap. V** and **VI** for more details). Individual state was described by a matrix including individuals' body size and sex.

A first Redundancy Analysis (RDA) quantified the contribution of phylogeny and habitat to morphological variation. It was indeed hypothesised that, since morphology is likely to be phylogenetically conserved and to respond plastically to environmental conditions, phylogeny and habitat may have an indirect impact on individual diet variation throughout morphology. It appeared that 25% of individual morphological variation within the fish assemblage were explained by phylogenetic distance between species, and only 1.5% by habitat. The unexplained part of morphological variation was extracted as the residuals of the RDA and then used in a second RDA-like analysis (db-RDA, **Chap VI**) that aimed at quantifying the direct effects of phylogeny, prey availability, unexplained morphological variation, and individual state on individual diet variation in the species assemblage. Altogether, the four factors explained 25% of individual diet variation. More precisely, prey availability, as well as phylogeny and individual state variables had a minor effect explaining less than 4% of variation. In contrast, morphological variation among individuals, independent from phylogeny and habitat, accounted for almost 18% of diet variation.

Surprisingly, a similar approach aiming at partitioning individual diet variation within each species, instead of within the assemblage, only found a marginal effect of morphology for a very few species. Individual body size and prey availability were the two factors most often involved in intra-specific diet variation, individual body size being the main one since it had a significant effect in 11 species out of 16 and contributed for a moderate to substantial fraction of variation (>7%) for 7 of them.

Chap. VI conclusions were that (i) phylogeny contributes a non-negligible part of individual morphological variation within the fish assemblages, but did not affect directly individual diet, (ii) morphology is a major determinant of individual diet variation and thus of trophic interactions in the fish community, and (iii) almost 75% of variance remains unexplained **(Fig. I.11)**. Part of this unexplained variation may be related to individual state that was possibly not represented precisely enough by individual sex and body size, but it is highly probable that a large proportion of unexplained diet variation is due to behavioural variation between individuals.

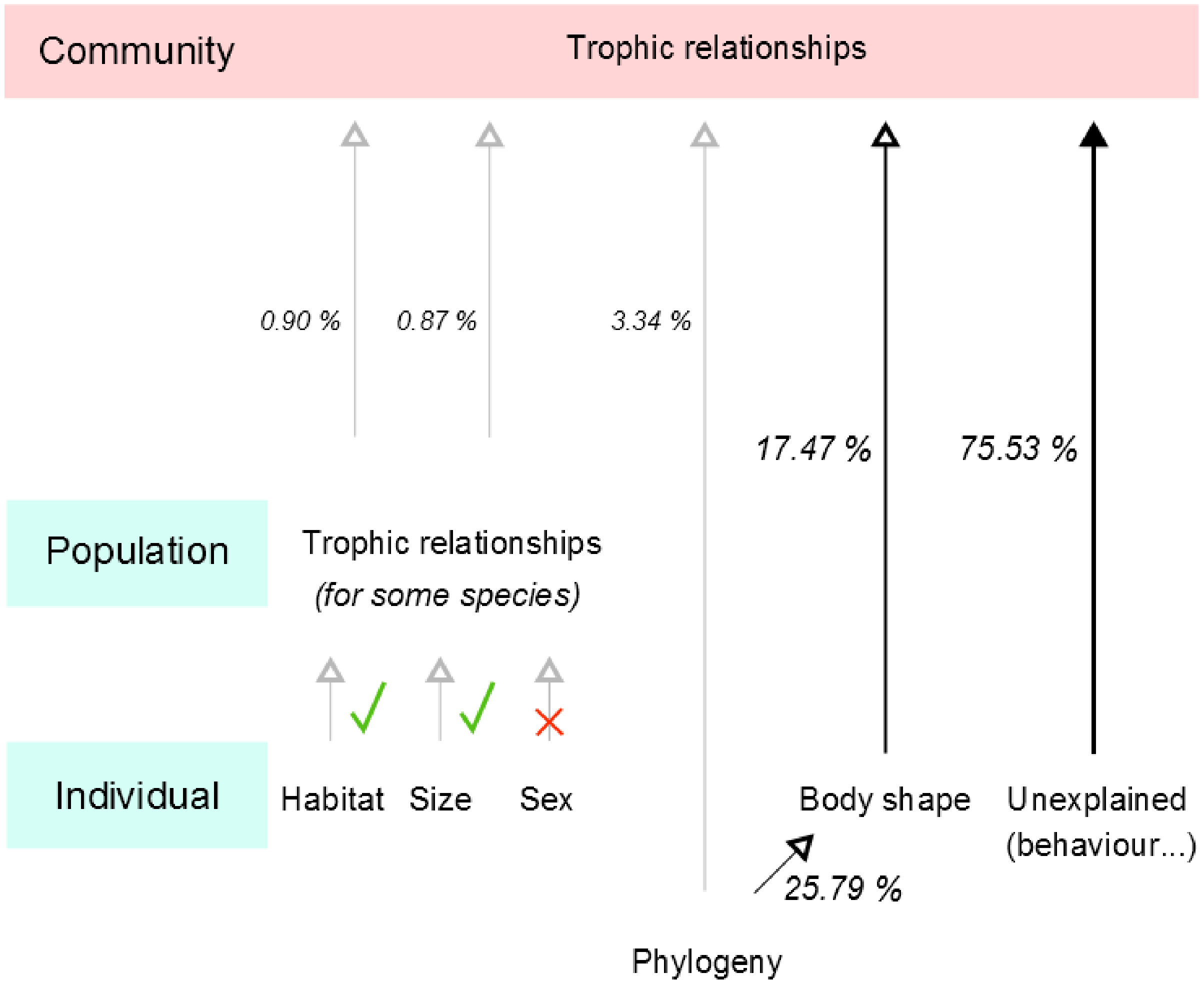


Figure I.11: Illustration of principal results from **Chap. VI** regarding the determinants of individual trophic relationships in the eastern English Channel fish community

I.8 A puzzling coincidence

In a relatively similar study aiming at assessing the relationship between ecomorphological proximity and diet similarity in a marine fish community, Albouy *et al.* (2011) also found 75% of variation unexplained. Although anecdotic, this puzzling coincidence calls for further scrutiny and comparison between these two experiments that found the same quantitative result using two different statistical approaches applied to two different ecosystems. Albouy *et al.* (2011) worked on 35 Mediterranean fish species and used a completely different analytical strategy. First of all, they used a species-level approach instead of an individual-level one. Secondly, instead of focusing on whole body morphology, they derived 13 functional traits related to food acquisition from 17 morphological measures that mainly concerned mouth (e.g. gape shape, protrusion…), eye (size and position), gill rakers, fins and gut length. Only 2 measures were related to the whole body, namely body transversal shape and body transversal surface. Finally, they investigated the relationship between ecomorphological trait dissimilarities and dietary dissimilarities between species using Generalized Dissimilarity Modelling, a multivariate extension of the Mantel approach.

In addition to these technical considerations, the ecosystems under study were highly contrasted. Albouy *et al.* (2011) collected fish species in a Marine Protected Area in the Mediterranean sea (Bonifacio Strait Natural Reserve, Corsica Island, France) whereas species of our study were sampled in a highly exploited marine area, the eastern English Channel. Beyond the fact that fish communities of the Mediterranean sea and of the English Channel are different, the Bonifacio Strait Natural Reserve is characterized by rocky and sandy substrates and *Posidonia oceanica* seagrass beds, a particular habitat that is not present in the English Channel. However, the Bonifacio Strait Natural Reserve and the eastern English Channel have relatively similar hydrodynamics. Both are indeed epicontinental marine areas characterized by strong currents along their coastlines caused by straits, the Bonifacio Strait and the Dover Strait, and their shallowness (< 60 m, Albouy pers. com., Gerigny *et al.* 2011). Basically, the Bonifacio Strait Natural Reserve and the eastern English Channel appear to have similar hydrodynamic conditions, but probably contrasted biotic conditions. This last point does not imply, however, that the two areas differ strongly in terms of biodiversity. They may even be relatively similar, in terms of biodiversity and maybe functioning, at a global scale (e.g. they both belong to the same large Marine Ecosystem, see **Chap. II**) Despite technical differences and different geographical areas, Albouy *et al.* (2011) and the present study mostly attribute the relatively moderate relationship between morphological and diet variation to behavioural versatility of fish, in accordance with Bellwood *et al.* (2006). A hypothesize would be that the level of behavioural versatility, and thus the strength of the relationships between morphology and diet, in fish species is somewhat related to the diversity in the community since diversity may partly reflect environment heterogeneity **(Fig. I.12)**. More precisely, fish in low diversity communities related to homogeneous environments, such as the pelagic zone, would not be very versatile since there are only a few prey items available (e.g. plankton in pelagos). Fish would then be morphologically specialized to forage of these items implying a strong link between morphology and diet. In moderate diversity communities associated with mildly heterogeneous environments hosting a larger diversity of prey, fish would tend to become versatile and begin to use a wide range of prey items irrespective of their morphology. In this case, the relationships between morphology and diet would be relatively low. Finally, in hot-spots of fish diversity and biodiversity in general, such as coral reefs, the environment and available prey items reach such an extreme level of diversity that fish would have the opportunity to morphologically specialize to foraging on different prey items, implying again a string link between morphology and diet. Although this hypothesis might be wrong, results of Albouy *et al.* (2011) and this study clearly call for more studies on the relationship between morphology and trophic interactions, notably in different ecoregions characterized by varying levels of environmental heterogeneity and diversity.

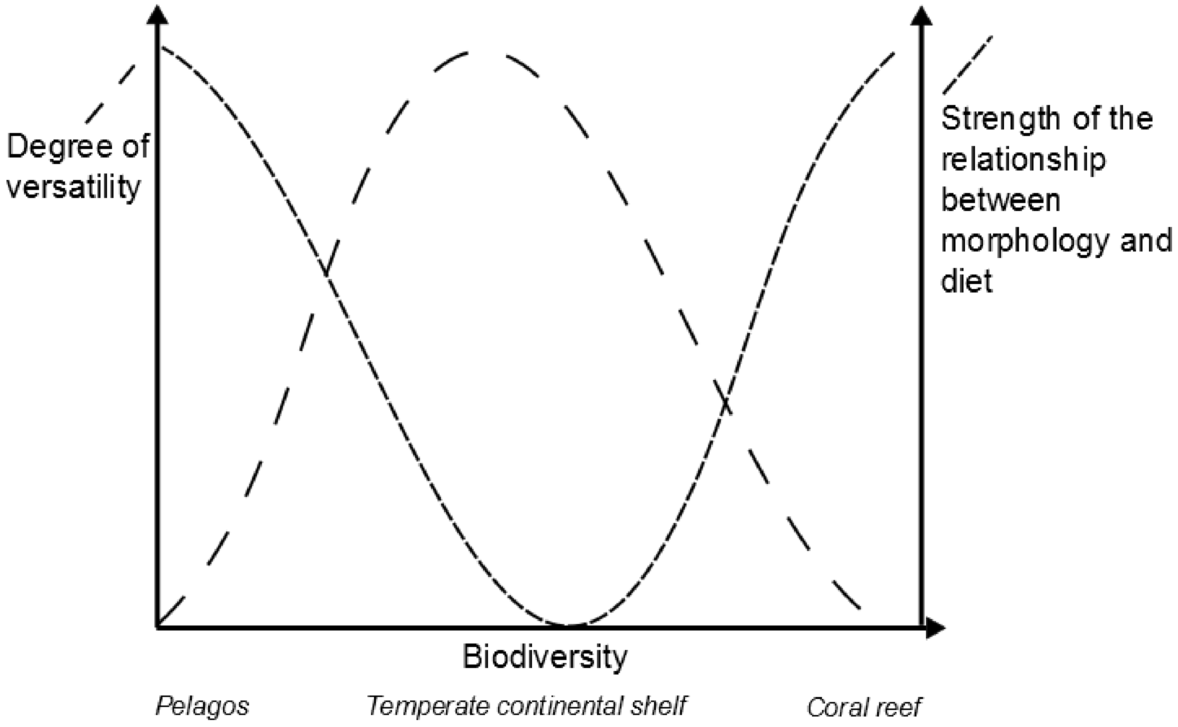


Figure I.12: Theory on the relationships between biodiversity, and behavioural versatility and the relationships between morphology in diet in fish.

I.9 Limits, conceptual foreground & perspectives

I.9.1 Limits of the sampling scheme

The main limitation in the sampling scheme used for this thesis relates to digestive tracts analysis. Individual fish were collected during a single survey in October 2009 and it would be legitimate to question the representativeness of a single month of a single year for depicting species diets and trophic relationships in the community (but see Cumulative Prey curves in **PhD ANNEXE 4** and Ferry & Cailliet 1996). Particularly, seasonal and inter-annual variability in environmental conditions is likely to affect specie diet. However, there are some evidences about temporal stability of several compartments of the eastern English Channel ecosystem. Firstly, the taxonomic composition of the fish community appeared stable for the last two decade (Auber, pers. com). Secondly, environmental conditions are relatively constant throughout the year in the whole sampling area up to the point that there is no isocline in summer, so the water column is homogeneous, and supposedly, the benthic community relatively stable (Cachera, unpublished data).

An ideal sampling scheme for diet studies consist in observations of an individual’s foraging decisions repeated over time (Araùjo *et al.* 2011). However, the drawback of using single individual observations such as stomach content data is compensated for when there are multiple prey items in stomachs, mostly because they represent multiple and independent capture decisions and are thus supposed to be a good representation of the overall diet of the individual (Araùjo *et al.* 2011). Furthermore, when comparing individuals (belonging either to the same species or to different species) such as in this thesis, the sampling must be spatially and temporally limited, since any heterogeneity in space and/or time would induce a difference in available prey items and thus introduce a bias in the comparison (Araùjo *et al.* 2011). All these points tend to support the idea that diet data used in this thesis are probably relevant to represent individual and species diet as well as trophic relationships involving the eastern English Channel fish community.

This conclusion does not exclude that it would be better to have a sampling scheme that takes temporal variability into account by collecting samples during other years and seasons. Diet data at different time point would allow to test for temporal stability in trophic relationships and thus in trophic network structure. Moreover, it may offer the opportunity to test for the theories regarding feeding behaviour, such as the competitive refugium theory (Robinson & Wilson 1998). If indeed a specialized morphology allows to turn back to a specialized diet when usual food resources are scarce, then it may be hypothesized that temporal variation in prey availability (because of seasonal migrations or anthropic exploitation for example) should reveal variation in the strength of the relationship between morphology and diet.

I.9.2 The importance of behaviour

Behaviour is supposed to be key for trophic interactions (Dall *et al.* 2012) but the apparent generalized feeding versatility of fish renders the prediction of their trophic ecology difficult. Behavioural versatility is considered as an important advantage, since it allows fish to respond to environmental changes (West-Eberhard 1989; Dall *et al.* 2012). It also promotes biodiversity by relaxing trophic competition (Bellwood *et al.* 2006), and tends to stabilize communities through behavioural-mediated indirect interactions (Bolker *et al.* 2003; Werner & Peacor 2003). Animal behaviour is known as "personality" (Bell 2007) and can sometimes take the form of opportunism. Opportunism is different from versatility since it occurs when a predator attacks a non-preferred prey species without prior intention (Cressman & Garay 2010). In contrast, versatility is the ability to attack a wide diversity of prey, depending on the environmental conditions, whether they be biotic or abiotic. A notable exception with regard to opportunistic behaviour are humans, since it happens when a rare resource or species is still exploited despite the fact that its exploitation is not profitable anymore (Branch *et al.* 2013).

I.9.3 From behaviour to ecosystem

Behaviour has both ecological and evolutionary implications. Ecologically, the direct effect of foraging behaviour is the consumption of a particular prey, and thus affects the top-down control exercised by predators on prey populations as well as competitive interactions with other species or conspecifics. Indirect effects of behaviour also exist and appear relatively strong, e.g. the modification of prey behaviour because of predator intimidation, a concept coined as the "landscape of fear" (Laundré *et al.* 2010). Foraging behaviour is described as a key factor for food web architecture (Beckerman *et al.* 2006; Lazzaro *et al.* 2009) and is even expected to dominate trophic cascade in food web, notably through behaviour-mediated interactions (Preisser *et al.* 2005). Consequently, behaviour is implicated in population dynamics and biotic interactions. Evolutionarily speaking, foraging behaviour may induce new morphological traits, either defensive or offensive (e.g. inducible defense, Harvell 1990; Clark & Harvell 1992), as expected from the Red Queen theory (Van Valen 1973, 1977), or changes in life-history (Stearns 1989). Versatility in feeding behaviour also promotes both prey and predator coexistence (Bellwood *et al.* 2006) and stabilizes communities (Bolker *et al.* 2003; Werner & Peacor 2003).

I.9.4 Conclusion

This thesis has demonstrated that morphology is one of the significant determinants of trophic interactions and that it can be used to assess trophic groups and functional groups **(Fig. I.13)**. But it has also reinforced the supposition of the importance of trophic versatility in fish in agreement with Bellwood et al. (2006) and Albouy *et al.* (2011). Further studies are needed to assess whether these conclusions are valid in other ecosystems, from tropical to polar marine systems, but also freshwater and terrestrial ones. It is possible that, for some systems, behaviour has lower importance and/or that ecosystem stability depends less on omnivory or versatility.

From an applied perspective, a next step would be to assess the impact of fish species loss in the eastern English Channel. We have learned from the theories of trophic cascade and Biodiversity Ecosystem Functioning that species local extirpation or collapse can have huge consequences on ecosystems. It is particularly true for marine systems where anthropic pressures are numerous and heavy. Chemical pollution of freshwater streams impacts nearshore ecosystems, extraction of resources can alter or destroy natural habitat, and overfishing drives species (especially top predator) to extinction (fishing down the food web) and can cause the collapse of coastal ecosystems (Pauly *et al.* 1998; Jackson *et al.* 2001; Duffy 2003; Halpern *et al.* 2008). In this context, there is a desperate need for scientists to understand better the dependency of ecosystem functioning on the composition of communities at the species and individual level and on phylogenetic, trophic, morphological and functional diversity, and to apply this knowledge to biodiversity and ecosystem conservation.

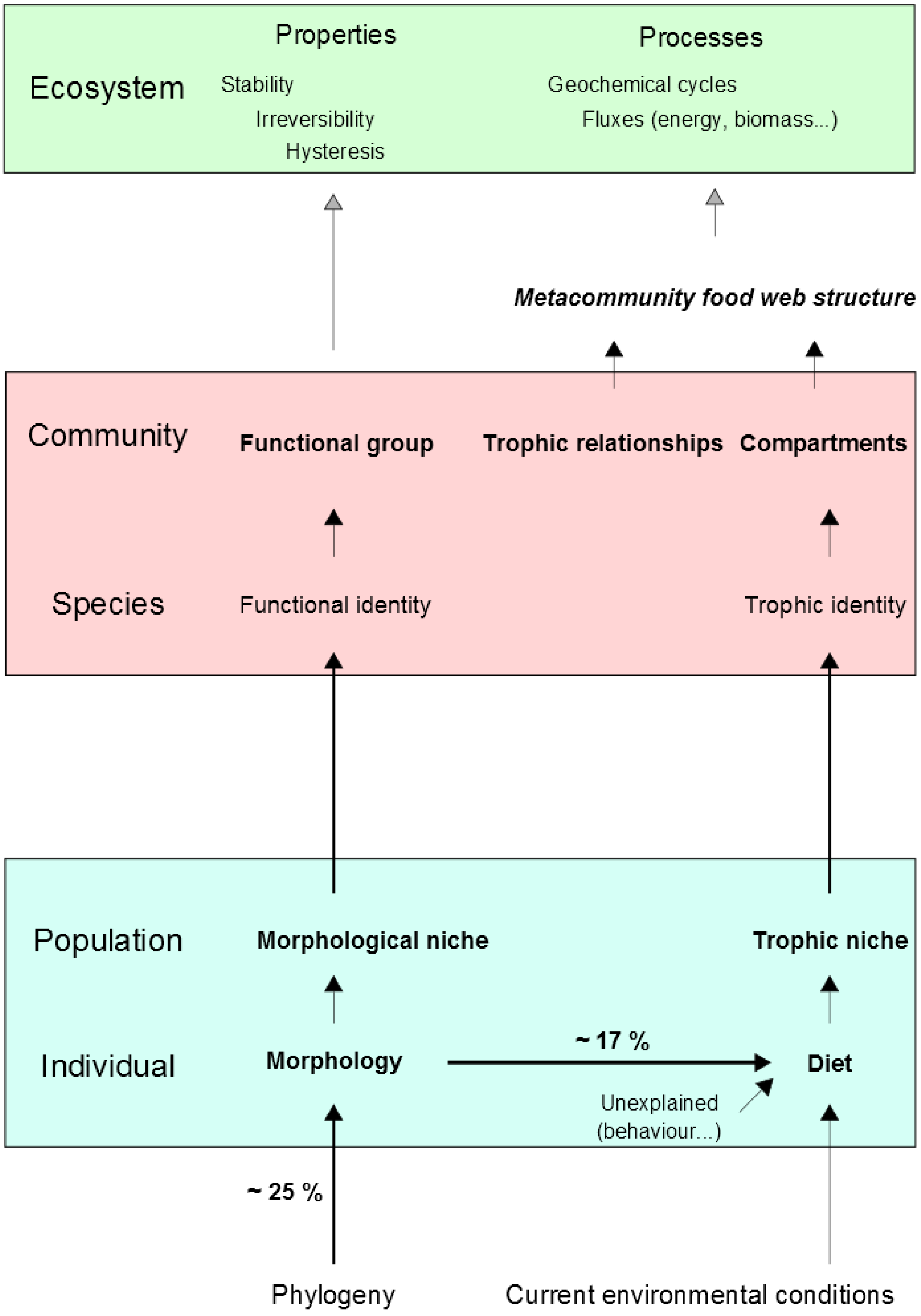


Figure I.13: Conclusive diagram summarizing the main results of this thesis.

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Chapter II System studied and sampling scheme

Louis cachera

II.1 The English Channel

The NOAA (National Oceanic and Atmospheric Administration) defined Large Marine Ecosystems (LMEs) as “areas of the ocean characterized by distinct bathymetry, hydrology, productivity and trophic interactions” (**Fig. II.1**). The English Channel belongs to the 24th LME and is located between the Atlantic Ocean and the North Sea. It is thus considered as a semi-closed epicontinental sea and as a transitional area between temperate and boreal regions (Sanvicente-Añorve *et al.* 2002).

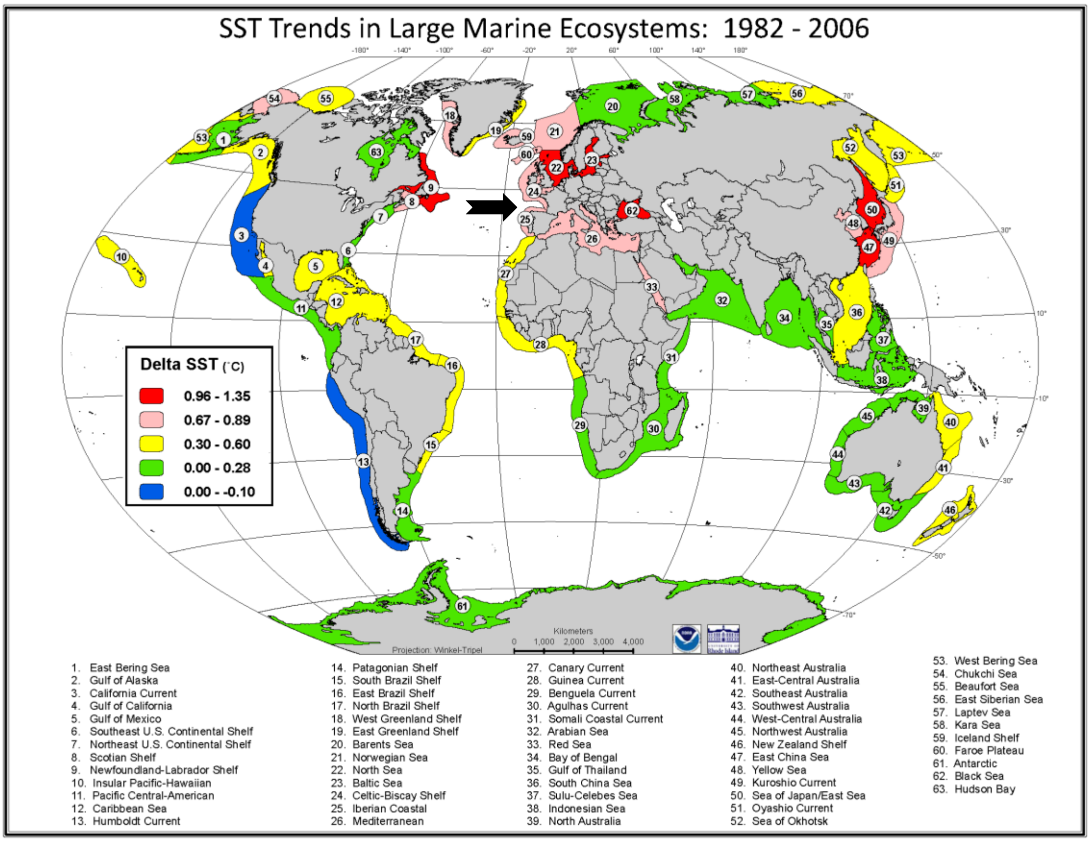


Figure II.1: Map of global trends in the evolution of the Sea Surface Temperature (SST) from 1982 to 2006. (English Channel is comprising in the Celtic-Biscay Shelf, #24). From NOAA 2013.

The English Channel is particularly shallow, with depth ranging from 30 m in the Dover Strait on the East end to 100 m on the West end. Coming from its western part, Atlantic waters are fast swelled over the shallow shelf and then enter in the North Sea via the Dover Strait. A smaller amount of waters from the North Sea is entering in the Channel along the English coastline. One of its characteristics is the presence of a coastal current from the Seine Estuary, that goes North along the French coasts (Gueguenaiat *et al.* 1993). Consequently, the English Channel is a macro-tidal environment, known for its strong tides and associated violent currents (Salomon & Breton 1993). This hydrologic regime determines sediment distribution, which basically comprises pebbles and gravels offshore, and homogeneous coastal sand banks (Foveau *et al.* 2013). This heterogeneous seabed allows the English Channel to host a wide diversity of habitats and species (no less than 200 taxa recorded during the Channel Ground Fish Survey in 2009, see also Foveau, 2009 for the benthic biodiversity).

With an increase in Sea Surface Temperature (SST) of 0.72 °C between 1982 and 2006, the English Channel is also one of the most impacted marine ecoregion by global change (**Fig. II.2,** Belkin, 2009). Like many temperate coastal ecosystems, the English Channel has also been exploited for decades (**Fig. II.2**). Beyond the fact that 20 % of the global marine traffic goes through the Dover Strait (400 to 500 ships by day), it is also a main fishing area in western Europe (approximately 4000 fishing vessels operate within the English Channel, Buléon & Shurmer-Smith, 2007; Pascoe & Coglan, 2002). Other strong anthropic pressures are present in the English Channel, namely aquaculture, extraction of aggregates, tourism, underwater cables, but also terrestrial pollution carried by rivers (**Fig. II.2**).

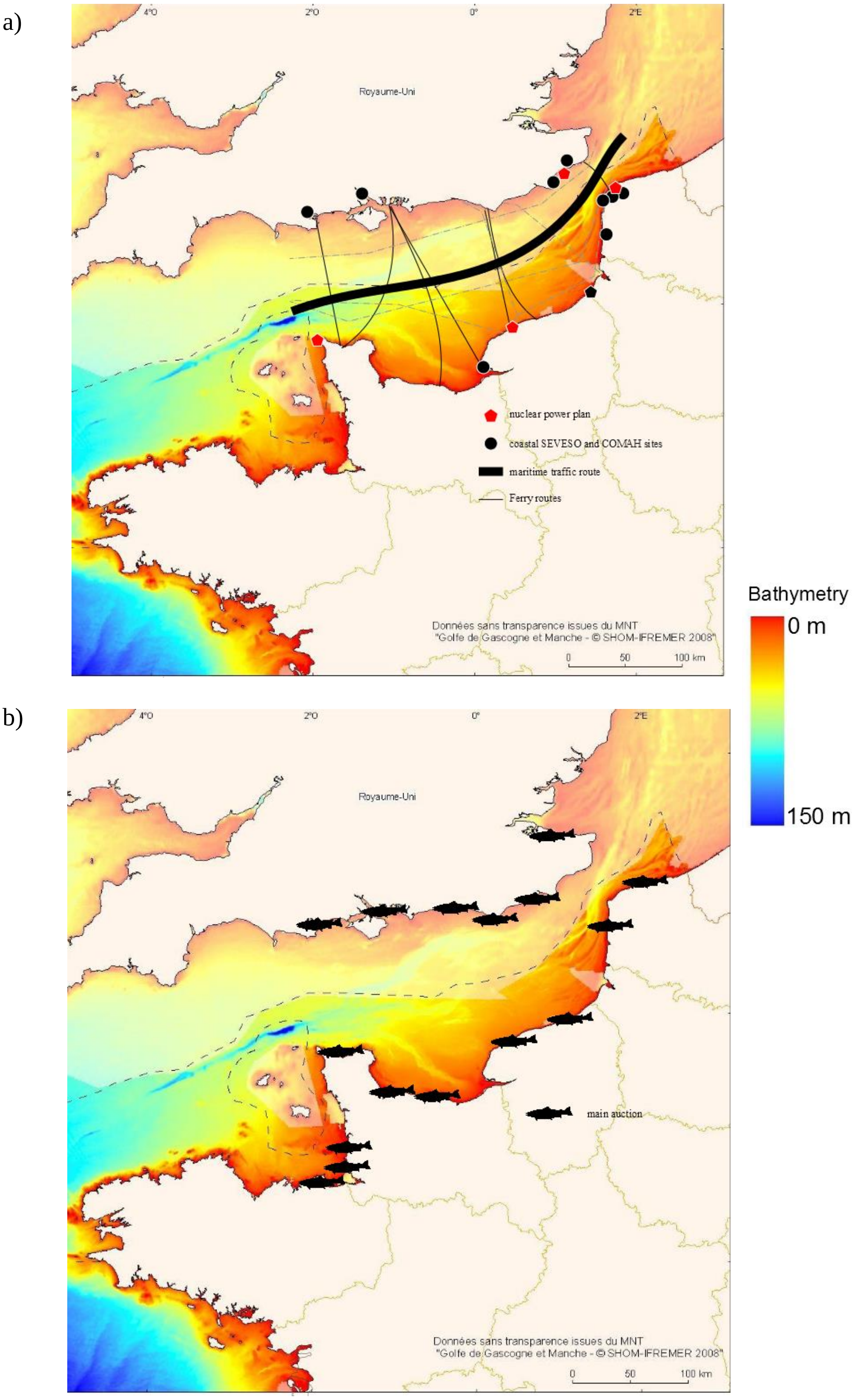


Figure II.2: Maps of a) Principal anthropic activities in the eastern English Channel. b) Main auctions for fisheries in the eastern English Channel.

II.2 Redundant aspects in Chapters' Materials and Methods

II.2.1 Sampling area and scheme: the Channel Ground Fish Survey

Figure II.3: The N/O Gwen Drez, length: 24.50 m, launched in 1976.

The Channel Ground Fish Survey (CGFS) is an annual scientific campaign conducted by IFREMER in October since 1988 on board RV "Gwen Drez" (**Fig. II.3**). It follows a spatially stratified sampling scheme, the area being subdivided in 15' x 15' rectangles where at least one haul is performed (**Fig. II.4).** Trawls of 30 minutes are towed at a speed of approximately 3.5 knots using a high opening demersal trawl (GOV) with a cod-end of 20 mm stretched mesh. At each sampling station, fish and cephalopod species are sorted, weighed, counted, measured (**Fig. II.4**) and (where relevant) sexed (with determination of maturity stage). For selected species, calcified structures (otoliths and/or scales are collected for ageing in the laboratory). Samples used in this study were collected during the 2009 survey. 100 out of 106 trawls were validated and sixteen species of fish (**Table II.1**), chosen to represent a wide diversity of habitats, morphologies, and feeding habits, were collected for this study. Following the capture, fish were identified, labelled, frozen on board with liquid nitrogen and kept frozen until further use.

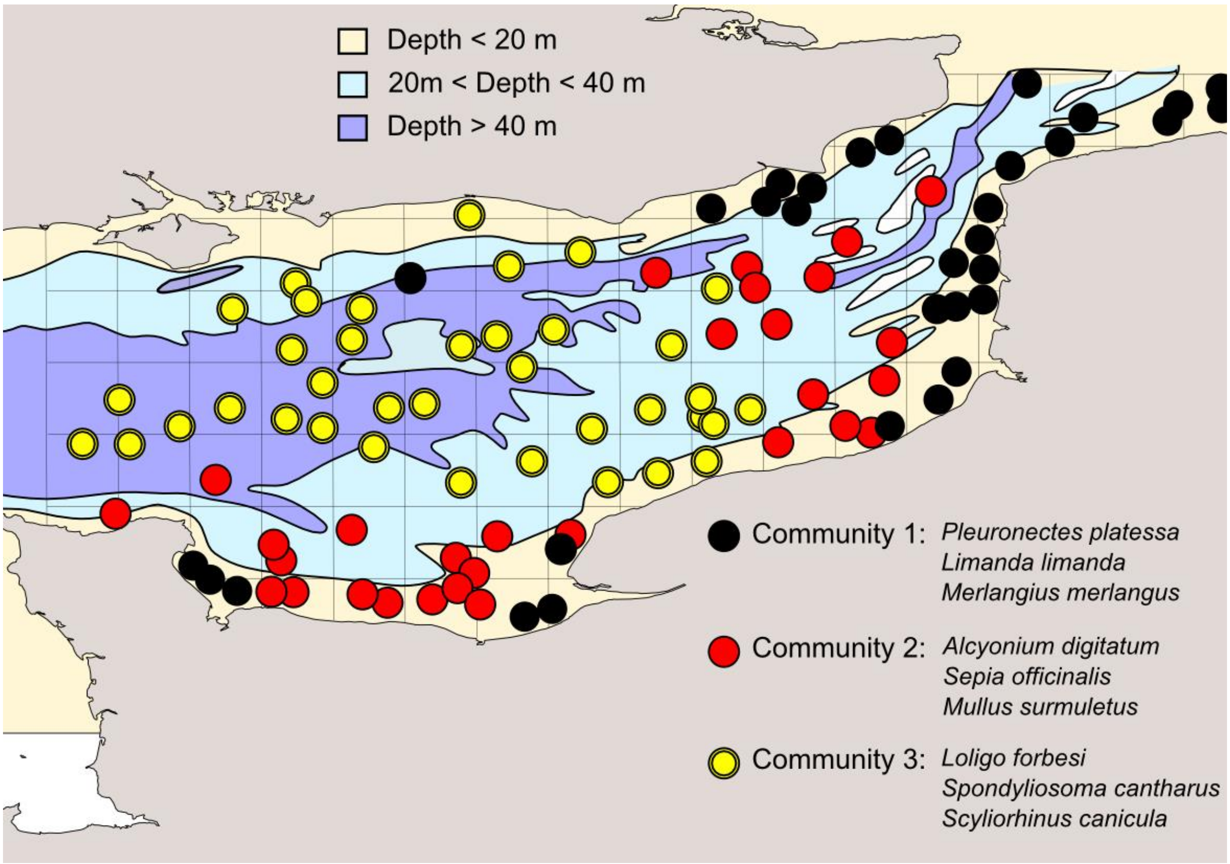


Figure II.4: Sampling area and sampling grid of the CGFS. Isobaths are represented to assess the limit of 20 m deep. 3 communities of invertebrates and vertebrates captured during the survey were defined by hierarchical clustering analysis on presence/absence data and characterised by 3 indicators species that were identified using the index of Dufrêne & Legendre (1997) (see **PhD ANNEXE 1**).

Table II.1: Table of fish species used in this PhD.

Scientific name	**Common name (fr)**	**Common name (en)**	**Name in the thesis**
Chelidonichthys cuculus	Grondin rouge	Red gurnard	**Red gurnard**
Chelidonichthys lucerna	Grondin perlon	Tub gurnard	**Tub gurnard**
Clupea harengus	Hareng	Atlantic herring	**Herring**
Dicentrarchus labrax	Bar	European seabass	**Seabass**
Gadus morha	Morue	Atlantic cod	**Cod**
Merlangius merlangus	Merlan	Whiting	**Whiting**
Mullus surmuletus	Rouget barbet	Surmullet	**Surmullet**
Mustelus asterias	Emissole tachetée	Starry smoothhound	**Smoothhound**
Pleuronectes platessa	Plie	European plaice	**Plaice**
Raja clavata	Raie bouclée	Thornback skate	**Skate**
Sardina pilchardus	Sardine	European pilchard	**Pilchard**
Scomber scombrus	Maquereau	Atlantic mackerel	**Mackerel**
Scyliorhinus canicula	Petite roussette	Smallspotted catshark	**Catshark**
Solea solea	Sole	Common sole	**Sole**
Sprattus sprattus	Sprat	European sprat	**Sprat**
Trachurus trachurus	Chinchard	Atlantic horse mackerel	**Horse mackerel**

II.2.3 Back in the laboratory and databases' creation

Geometric morphometrics

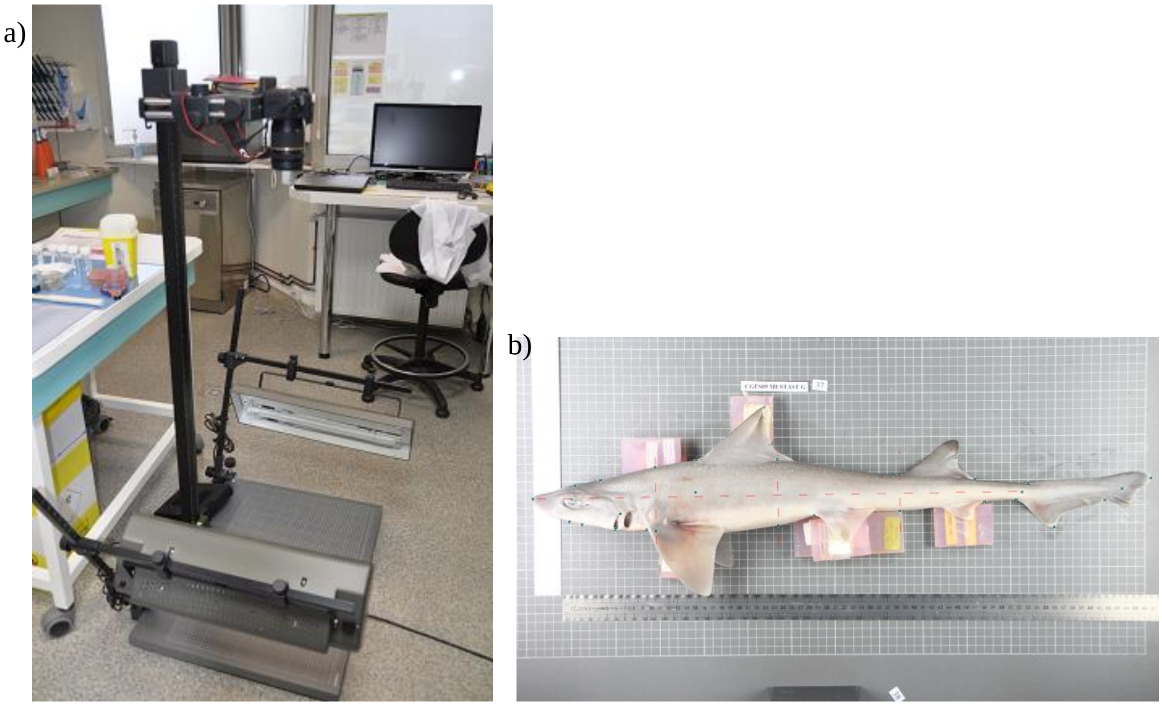


Figure II.5: a) Camera stand and camera in the trophic laboratory. b) Original picture of a starry smoothhound (*Mustelus asterias*) and captured (semi-)landmarks.

Each fish was defrost, measured, and sexed. A numerical picture of each individual was taken with a camera (Nikon® D7000) positioned at 140cm high with a Kaiser® camera stand (**Fig. II.5 a**). 22 landmarks and semi-landmarks along the whole body were captured from the picture using ImageJ®. (Semi-)Landmarks, captured on 833 fish pictures, were homologous between species and individuals, and were chosen to fit the shape of the whole body. Landmarks (points 1 to 3, 7 to 13, and 17 to 22; **Fig. II.5 b**) corresponded to specific anatomical features and semi-landmarks (points 4 to 6 and 14 to 16; **Fig. II.5 b**) were constructed by dividing the individual's standard length in quarters (see **PhD ANNEXE 2**).

Using (semi-)landmarks' coordinates as morphological data, an inter-specific Generalized Procrustes Analysis (GPA) was performed with all individuals of all species (Goodall 1991; Dryden & Mardia 1998). GPA scales, translates and rotates individual (semi-)landmarks'

The legend of Procrustes

In Greek mythology, Procrustes was one of the sons of Poseidon who lived on Mount Korydallos. He used to invite people passing by to stay for the night. As they laid for some rest, Procrustes forced them to fit on his iron bed. If the passer-by was too tall, Procrustes amputated him with his hammer, and if he was too small, he stretched him to death. Nobody ever fit, as Procrustes had in fact two different beds. He was captured and killed by Theseus, who forced Procrustes to fit in his own bed, in the same way he had done to many strangers.

configuration to minimize the sum of squared distances between pairs of homologous (semi-)landmarks (superimposition, **Fig. II.6**). The distances between individual (semi-)landmarks after superimposition and the resulting mean landmark configuration, called Procrustes residuals, were then used to as inter-specific morphometrical data. The multi-dimensional morphometrical space resulting from Procrustes residuals is then called morphospace. Intra-specific GPAs were also performed for each species separately. All GPAs were performed with the package “shapes” (Dryden 2012) of the software R (R Core Team 2012).

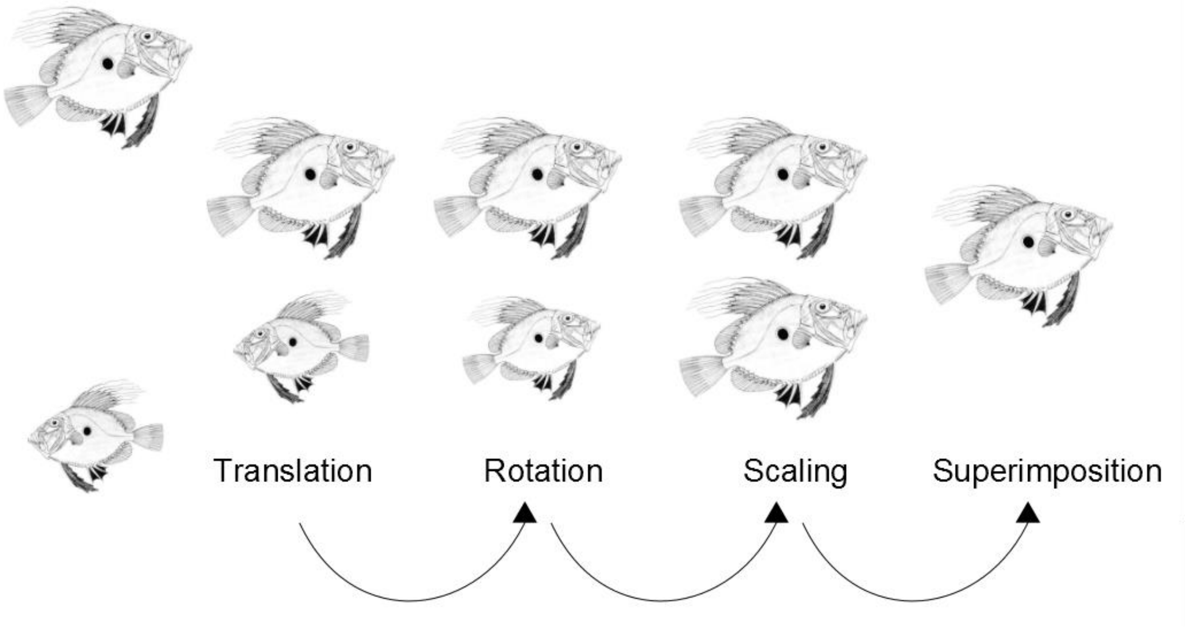
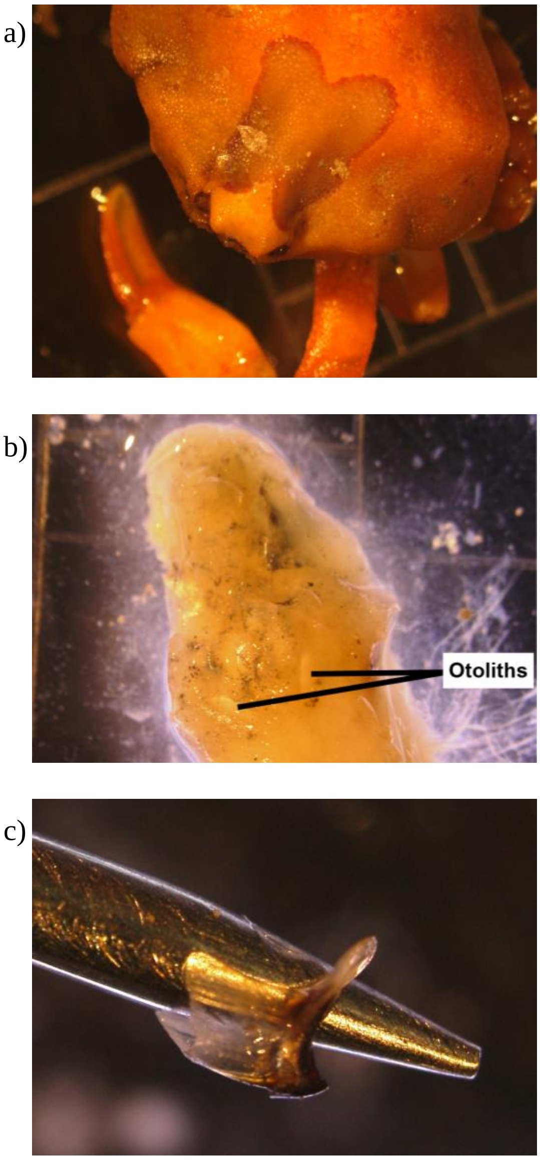


Figure II.6: Principles of the Procrustes Analysis.

In **Chap. V**, only the eleven species of teleost round fish (i.e. *Chelidonichthys cuculus, Chelidonichthys lucerna*, *Merlangius merlangus, Gadus morhua, Trachurus trachurus, Sprattus sprattus, Sardina pilchardus, Clupea harengus, Scomber scombrus, Mullus surmuletus* and *Dicentrarchus labrax*) were used, since it is generally advised, when creating a morphospace, to use “comparable” species. On the contrary, since biostatistical analyses in **Chap. VI** were not based on the creation of the morphospace, all sixteen species were under study.

Digestive tracts analysis

After the numerical picture was taken, each fish was dissected to extract its digestive tract and the contents was removed and stored in a Petri-dish for analysis (**Fig. II.7**).



Limits and advantages of digestive tracts analysis

- limited window of time (snapshop)
- time consuming
+ finest taxonomical identification of prey items
+ multiple prey items represent multiple capture decisions
+ representativeness of the species’ diet can be mathematically assessed (permutation and cumulative prey curve, see **PhD ANNEXE 4**)

Figure II.7: Illustrative pictures of prey items found during digestive tracts’ content analysis. a) *Ebalia tumefacta*, b) digested gobie (*Gobius sp*) with otoliths, c) beak of *Rossia macrosoma*.

Prey were identified to the lowest possible taxon under a stereo microscope Olympus SZX16©, sorted, counted and weighed (0.1 g) in 853 non-empty stomach. 96 empty digestive tracts were excluded from analyses. Preys were grouped in 41 categories combining taxonomic level and functional characteristics (see **PhD ANNEXE 3**). Then, for each of the 853 individuals, the proportion of each prey category in diet, p_{ik}, was calculated on the basis of the Geometric Mean (GM) of prey number and weight such as:

$$p_{ik} = \frac{\sqrt{W_{ik} \times N_{ik}}}{\sum_{i=1}^{16} (\sqrt{(W_{i'k} \times N_{i'k})})} = \frac{g_{ik}}{\sum_{i'} g_{i'k}}$$

where W_{ik} and N_{ik} are the weight and the number of prey of category i in the stomach of individual k. Geometric mean was used in order to compensate for prey importance in weight and number. Combining these two aspects is considered effective in depicting dietary importance of prey categories, since it allows us to take into account energy consumption (prey biomass, W_{ik}) and foraging behaviour (prey count, N_{ik}, Hyslop, 1980).

It is the very first time that Geometric Mean is used in order to estimate prey proportion, whether it be at individual or species level.

In **Chap. VI**, 833 individuals were used after exclusion of empty stomach and individuals with unusable pictures.

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Chapter III Relative impacts of ontogeny and community composition on a marine fish community's trophic network structure

Josette Cachera

III.1 Abstract

A trophic network is generally organized into compartments, i.e. groups of strongly connected species with weak trophic relationships to other groups. This organization results from asymmetrical strengths of trophic relationships between species. Understanding a trophic network structure is necessary to ascertain determinants of trophic relationships and their impacts on compartmentalization. Two main determinants of trophic relationships are species diversity and trophic identity. Diversity changes with community composition and trophic identity may vary across the species life stages, e.g. in the case of an ontogenetic trophic niche shift. Consequently, a trophic network structure would be determined by (i) dietary change with size (ontogenetic diet shift), (ii) spatial variation of evolved species. This study investigated the impact of size and of community composition on the structure of a marine trophic network. Trophic identities of 16 fish species were described, and variation in trophic relationships due to size and the interaction between size and depth were investigated. Depth was used as a proxy for spatial variation in community composition. The computation of compartments, and of several network metrics, allowed us to describe and compare the structure of the metacommunity trophic network, and two community sub-networks. It highlighted (i) the minor importance of ontogenetic diet shift in the compartmentalization of the trophic network, (ii) the importance of species trophic identity, omnivory in particular, and (iii) the hierarchical architecture of a marine trophic network. A metacommunity topology was clearly depicted with pelagic and benthic components, and local benthic communities, all connected by mobile predators such as fish.

III.2 Introduction

A trophic network is composed of a set of trophic relationships between species within a community, i.e. predator-prey relationships. Trophic network structure depends on several factors, mainly specific diversity and species' trophic identity that determine trophic interactions' diversity and strength (Rooney & McCann 2012). Diversity is defined here as species composition and relative abundance in a community, following Hooper *et al.*(2005), while a species' trophic identity is defined as its set of predators and prey items (Cohen & Briand 1984). Consequently, a trophic network structure should change if species' diversity and trophic identity, and thus trophic relationships, vary. Several studies have highlighted that trophic relationships tend to have different strengths (i.e. asymmetric) within a network, which in fact induces a non-random structure of studied trophic networks (Montoya *et al.* 2006). In these studies, groups have been described as compartments, with few strongly connected species that have many, but weak trophic relationships with species from other groups (Krause *et al.* 2003; Newman 2006; Belgrano *et al.* 2009). This asymmetrical structure has been proven to reduce trophic cascade and potentially increase the stability of the ecosystem (McCann *et al.* 1998; Krause *et al.* 2003; Rooney & McCann 2012). Consequently, it is of particular importance to point out what implies: a variation in trophic relationships; how it may impact the organization of compartments; and what would be the resulting change of the structure of the trophic network.

A main determinant that may imply a variation in trophic relationships is the fact that many organisms change their trophic identity, by modifying their predators and prey items, through life stages. When focusing on trophic relationships with prey, it has merely been described that species generally tend to change their diet with size, i.e. ontogenetic diet shifts (Polis 1984; Pires *et al.* 2011), often related to an ontogenetic habitat shift. It may thus be hypothesised that, if a species exhibits an ontogenetic diet shift, it could also change its compartment with size, and modify the structure of the trophic network. Another determinant of trophic relationships (and consequently of trophic network's structure) is change in the specific composition of the evolved community, generally related to a change in habitat (Thompson & Townsend 2005). Since species diversity and its trophic identity establish trophic relationships, it is expected that a spatial change in community composition would change available prey, predators, and competitors, and consequently modify the trophic network's structure (Petchey *et al.* 1999; Downing & Leibold 2002).

To characterise trophic network structure, authors have developed several metrics, such as species richness and connectance (fraction of possible link out of all the possible ones, Dunne *et al.* 2004). These metrics have notably been used to compare terrestrial, freshwater, and marine food webs structures, and to assess the potential stability of such networks to species loss (McCann *et al.* 1998; Dunne *et al.* 2002; Krause *et al.* 2003). However, because computations of these metrics necessitate large databases, these studies have had no choice but to use predictive models or rely on meta-analysis of data from different origins in order to be able to examine trophic network structures. As a consequence, it has not been possible to investigate the determinant of trophic network structure, as it has necessitated individual-level data to assess the impact of size and habitat on trophic relationships variation.

Marine ecosystems have several characteristics that would allow the ascertaining of the determinism of a trophic network structure. First, marine ecosystems hold a high proportion of omnivory (Fagan 1997; Bascompte *et al.* 2005) that are involved, by definition, in many trophic relationships, and apparently give particular properties to marine network structure (high connectance, Link 2002; Dunne *et al.* 2004; Belgrano *et al.* 2009). Then, marine species are well known to exhibit ontogenetic diet shift (Link 2002), as they tend to be coastal at youth and offshore at adult stage. A high proportion of species concerned with ontogenetic diet shift may impact the structure of the trophic network (Ingram *et al.* 2011). Finally, marine ecosystems are generally structured by depth (Majewski *et al.* 2013), with pelagic and benthic communities intermingled in shallow waters, and more separated in deeper waters. Consequently, pelagic and benthic compartments may be more contrasted as depth increases. Furthermore, the benthic species diversity is higher than the pelagic one, and in general, benthic species, particularly invertebrates, have a restricted living area. The benthic community is thus supposed to be structurally complex with several local patches of diversity (Raffaelli *et al.* 2003; Quevedo *et al.* 2009). A hypothesis would be that a marine trophic network may exhibit structural variation along a coast-offshore gradient related to depth and benthic diversity. However, many higher-order predators forage on both pelagic and benthic communities, and move between prey patches within their home range. They allow the linking of pelagic and benthic communities, and local benthic communities between them. This pattern is an illustration of a trophic metacommunity, where two or more communities are trophically linked by movements of mobile predators (Rooney *et al.* 2006; Pillai *et al.* 2011). It may then be suggested that, in marine trophic metacommunity, mobile predators connect local prey communities and that trophic networks exhibit a hierarchical topology.

To supplement the evident lack of investigations into the implications of species identity and diversity on trophic relationships in marine ecosystems, this study’s first aim was to estimate the impact of organism’s size (ontogenetic identity shift) and spatial variation in community composition on individual trophic relationships. To further complete this goal, network metrics in an intra-system comparison of trophic network’s topology were used. A large database of digestive tracts was employed to quantify trophic relationships’ strength between 16 focal fish species and 41 prey categories. Digestive tract analysis allows us to identify precisely a prey species, and is it considered as a relevant representation of a species’ diet and strength of trophic relationships when several individuals’ tracts are sampled (Araùjo *et al.* 2011). It was hypothesised that: (i) ontogenetic diet shifts of species impacts on the structure of the trophic network (notably compartmentalization), and (ii) the structure of the trophic network would exhibit spatially-based variation related to depth due to changes in community composition and in species’ interactions, revealing in effect, a trophic metacommunity network. Network metrics were then used in order to compare the structure of the metacommunity network, and any, local communities’ networks.

III.3 Materials & Methods

III.3.1 Sample collection

Sixteen fish species, chosen to represent a wide diversity of trophic characteristics and further referred to as “focal fish species”, were collected in the eastern English Channel during the Channel Ground Fish Survey (CGFS) operated by IFREMER in October 2009 (**Fig. III.3.1**). Fish were caught on board RV “Gwen Drez” by towing a high opening demersal trawl (GOV) with a cod-end of 10 mm stretched mesh for 30 minutes at a speed of approximately 3.5 knots. A spatially stratified sample scheme was used, the area being subdivided into 15' x 15' rectangles in which the GOV trawl was fished at least once (**Fig. III.3.1**). Following their capture, focal fish species were identified and individuals were labelled, frozen on board with liquid nitrogen to stop digestion, and kept frozen until further use. In the laboratory, the fish were defrosted, dissected to extract their digestive tract and the contents spread and kept in Petri dishes for analysis.

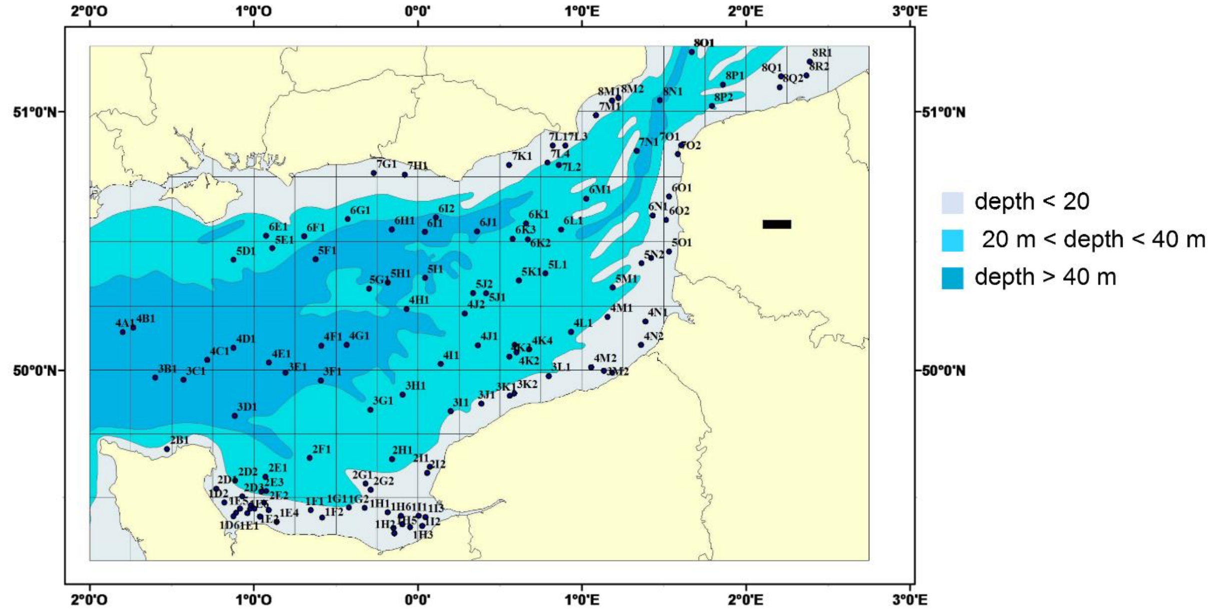

Figure III.1: Map of the area covered by the Channel Ground Fish Survey with trawls' location. Isobaths are represented to assess the limit of 20 m deep.

III.3.2 Digestive tract analysis

Prey were identified to the lowest possible taxon under a stereo microscope Olympus SZX16©, sorted, counted and weighed (0.1 g) in 853 available and non-empty digestive tracts. 96 empty digestive tracts were excluded from analysis. Prey items were then grouped in 41 categories combining taxonomic level and functional characteristics (see **PhD ANNEXE 3** for a complete description of prey categories). Then, for each focal fish species, the proportion p_{ij} of each prey category i in the diet was calculated on the basis of the Geometric Mean (GM) of prey number and weight such as:

$$p_{ij} = \frac{\sqrt{W_{ij} \times N_{ij}}}{\sum_{i'} (\sqrt{(W_{i'j} \times N_{i'j})})} = \frac{g_{ij}}{\sum_{i'} g_{i'j}},$$

where W_{ij} and N_{ij} are the total weight and the total number of prey categories i in the diet of focal fish species j, respectively. We used GM to calculate prey category proportion in the fish's diet as a new index to compensate for prey importance in weight and number. Combining these two aspects is considered effective in depicting dietary importance of prey categories, since it allows us to take into account energy consumption (prey biomass, W_i) and foraging behaviour (prey count, N_i) (see Hyslop 1980 for discussion).

Fish species diets

Trophic niche breadth was determined for each focal fish species using Levin's index:

$$B_j = \frac{1}{\sum_i p_{ij}^2},$$

It tends to 0 when the species has a narrow niche breadth (feeds only on one prey category), and increases with niche breadth (increasing diversity of food resources, Levin 1968). Levin's index has only been presented here, since other classical indices, such as Shannon-Wiener or Pielou indices of diversity, co-varied with Levin's.

Dietary specialization of focal fish species was quantified with the Proportional Similarity index (PS_j), calculated as follow:

$$PS_j = 1 - 0.5 \sum_i |p_{ij} - q_i|,$$

with $q_i = \frac{\sum_j \sqrt{W_{ij} \times N_{ij}}}{\sum_{i'} \sum_j \sqrt{W_{ij} \times N_{ij}}} = \frac{\sum_j g_{ij}}{\sum_{i'} \sum_j g_{i'j}}$, the proportion of prey category i in all focal species' diet.

PS_j, first proposed by Feinsinger *et al.* (1981), takes a value close to 1 when the species eats a lot of prey in the same proportion as all species taken altogether and considered as representative of prey availability, and so is considered as a generalist. It tends to 0 when the species has eaten only a subset of prey, and so is considered as a specialist. By making no assumption on resources distributions, PS_j appears to be one of the most robust estimators for trophic specialization (Bolnick *et al.* 2002).

Fish species trophic level, based on digestive tracts, was estimated following (Cortes 1999) as:

$$TL_j = 1 + (\sum_i \frac{W_{ij}}{W_j} \times TL_i),$$

where $\frac{W_{ij}}{W_j}$ is the proportion in weight of the i^{th} prey category in fish species j's diet, and TL_i is the trophic level of the i^{th} prey category calculated from nitrogen stable isotopes analysis ($\delta^{15}N$) in recent literature (see **PhD ANNEXE 3** for sources). Nitrogen stable isotopes analysis ($\delta^{15}N$) is commonly used to assess the trophic level of an organism. Its abundance in the predators' tissues is in fact typically 3.4 ‰ greater than that in their prey's tissues, so the isotopic signature of the consumer, compared to an appropriate isotopic baseline, allows the estimate of its trophic position (Peterson & Fry 1987; Post 2002).

A hierarchical clustering, using Ward's method and Euclidean distance, was applied to previous indices (B_j, PS_j &TL_j) to determine focal fish species with similar trophic characteristics.

III.3.3 Principle of analysis

A full factorial approach was used to investigate the impact of space and size of trophic relationships' variation. Spatial variation in community composition was assessed by depth, which appeared as a relevant proxy for the biocenosis and implicitly for related environmental conditions in continental marine ecosystem (Majewski *et al.* 2013). Individual size was used to describe the ontogenetic effect on variation in trophic relationships (ontogenetic diet shift). As depth was always significant in combination with size, it was decided to analyse trophic relationships and structure of trophic network including or size, or depth and size together. See **Fig. III.2** for analytical procedure.

III.3.4 Investigating the importance of spatial variation and ontogenetic diet shift

In order to assess the spatial change in community composition, a Multivariate Regression Tree (MRT, De'ath 2002) was applied to vertebrates and invertebrates species' presence-absence data recorded during CGFS 2009 under the constraint of depth. MRT is a clustering method that minimizes within-cluster sums of squares under the constraint of an explanatory variables - here depth (Borcard *et al.* 2011). It was considered that the depth defined by the first branch in the MRT was the limit between shallow and deeper communities. A change in community composition was detected by the MRT at a depth of 20 m (see **Fig. III.2** for analytical procedure and **ESM III.1**). A second change was detected at a depth of 38.5 m, but computation of compartments (described below) was not possible because of a loss of statistical power, and thus only the discrimination of community composition at 20 m deep was kept for further analyses.

In a second step, to figure out if ontogenetic diet shift appeared at the scale of the whole eastern English Channel, or at a finer scale, i.e. within shallow or deeper community, three successive db-RDA were applied for each focal fish species: (i) a db-RDA implying the categorical factor "depth" ("A" for above 20 m and "B" for below 20 m) and the continuous factor "size" (individual diet ~ depth + size + depth and size); (ii) a "shallow db-RDA" with individuals caught above 20 m (individual diet ~ size); and (iii) a "deeper db-RDA" with individuals caught below 20 m such (individual diet ~ size). See **Fig. III.2** for analytical procedure. db-RDA, i.e. distance-based Redundancy Analysis, is considered as the most robust equivalent of a RDA when data imposes Bray-Curtis distance's use (Legendre & Anderson 1999). This distance is semi-metric and considered as the best-known ecological distance for species abundance data (or prey abundance data in dietary study's case). Stepwise model selections, based on variable significance assessed by permutation tests, were performed to objectively select the subset of significant explanatory variables that accounted for almost the same amount of variance as the total set (reduced model). A Holm correction was then applied to all P-values obtained from permutation tests from db-RDA in order to account for multiple comparisons across the 16 focal fish species.

For focal fish species that exhibited a single effect of size, these were split into "small" and "large" individuals, regarding if they were above or below the critical size, respectively. This critical size, when the ontogenetic diet shift occurred, was detected with MRT applied to individual's diet (p_{ik}) under the constraint of individual size. For species that exhibited a combined effect of both size and depth, individuals were first split into groups of "shallow" individuals (above 20 m) and "deeper" individuals (below 20 m). Then, if a size effect remained significant in “shallow” or “deeper” db-RDA, the corresponding subset of individuals were split again into “small” and “large” individuals, following the same approach as described previously (MRT constrained by size). In order to assess that detected effects of size and depth were not due to differences in size ranges above and below 20 m (e.g. small individuals along coast and larger individuals offshore), complementary t-tests between sizes of individuals caught above and below 20 m were performed. Only four out of 16 focal fish species had a significant different mean size between shallow and deeper communities, and three of these were not detected by db-RDA as having effects of size and depth on trophic relationships, assessing the power of our experimental design. See **Fig. III.2** for analytical procedure

III.3.5 Structure of the trophic network

Diets were considered as a quantification of trophic relationships’ strength between focal fish species and prey categories, and consequently used to compute trophic compartments, trophic network and to calculate related network’s metrics. Compartments were computed using modularity - a method that separates two subsets of nodes in a network when their links are less numerous than expected by chance (random distribution of links). In this case, it allowed the detection of densely connected subsets of nodes (here focal fish species), called modules, in a network (here trophic network) without *a priori* on the number and size of modules (Newman 2006). Computation of modules on fish diets was used to determine trophic compartments, their specific composition (focal fish species), their dietary characteristics (prey categories), and then to assess the structure of the trophic network. Network metrics were also calculated, namely: linkage density (*D*) (number of link L per species S, $D = L/S$); connectance C (proportion of link realised compared to all potential links, $C = L/S^2$); nestedness (a species-level property, which measures to what extent a specialist species consumes a subset of prey, also used by a generalist species); and modularity (a community-level property measuring the compartmentalization of the network, i.e. the presence of subsets of species having many interactions among themselves, but few with species belonging to other modules). See **Fig. III.2** for analytical procedure

The structure of the metacommunity trophic network was investigated by computing trophic compartments, graphically assessing the topology, and calculating metrics, based on species’ diet and diets of subsets of “small” and “large” individuals for focal fish species that exhibited a single effect of size in previous db-RDA. Shallow and deeper communities’ trophic networks were also computed, based on diets of “shallow” and “deeper” groups of individuals of focal fish species, and, for species exhibiting a combined effect of both size and depth (depending on previous db-RDA results), diets of subsets of “small” and “large” individuals. Again, trophic compartments, topology, and network metrics (linkage density D, connectance C, nestedness and modularity) were computed to characterise and compare networks. It is important to notice that three focal fish species, namely smoothhound, catshark and sprat, were never caught above 20 m, and thus considered as absent in shallow waters. However, it was decided to keep this difference in fish species in order to correctly describe trophic networks in shallow and deeper waters.

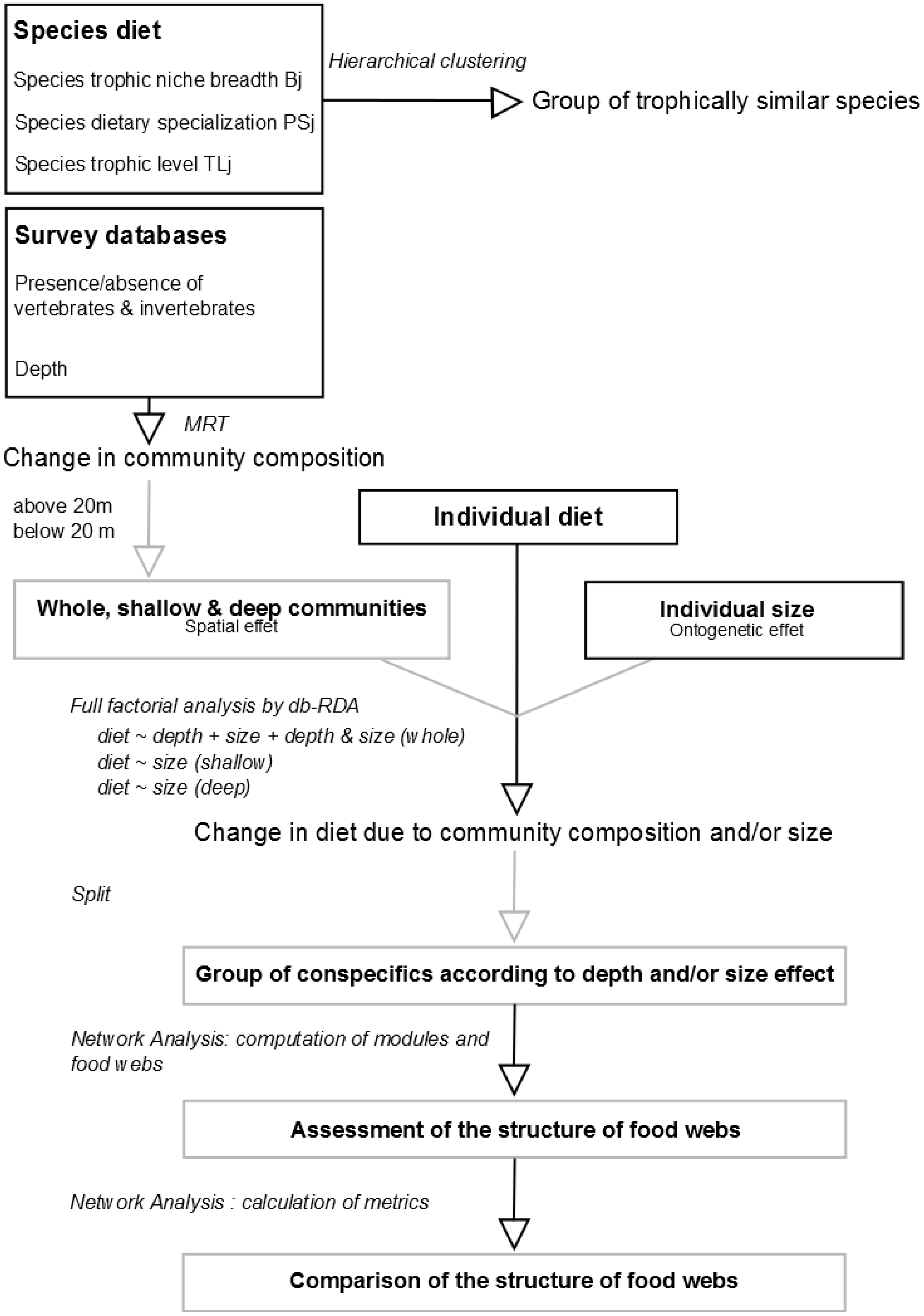

Figure III.2 : Scheme of analytical strategy.

Packages “mvpart” (Therneau *et al.* 2012), “vegan” (Oksanen *et al.* 2012) and “bipartite” (Dormann et al. 2008) from the software R (R Core Team 2012) were used to perform analyses, as well as the software Network3D (Yoon *et al.* 2004; Williams 2010) for network metrics' computation.

III.4 Results

III.4.1 Fish species' diets and trophic identities

The hierarchical clustering of focal fish species' trophic characteristics (B_j, PS_j & TL_j, see **ESM III.2**) roughly indicated five similar groups (**Fig III.3 a**). These groups were essentially discriminated by their values of B_j and PS_j since the species trophic level (TL_j) was medium for all focal fish species, and thus not discriminating (mean TL_j = 4.06, min TL_j = 3.51 and max TL_j = 4.67), and further not described (**Fig III.3 a**).

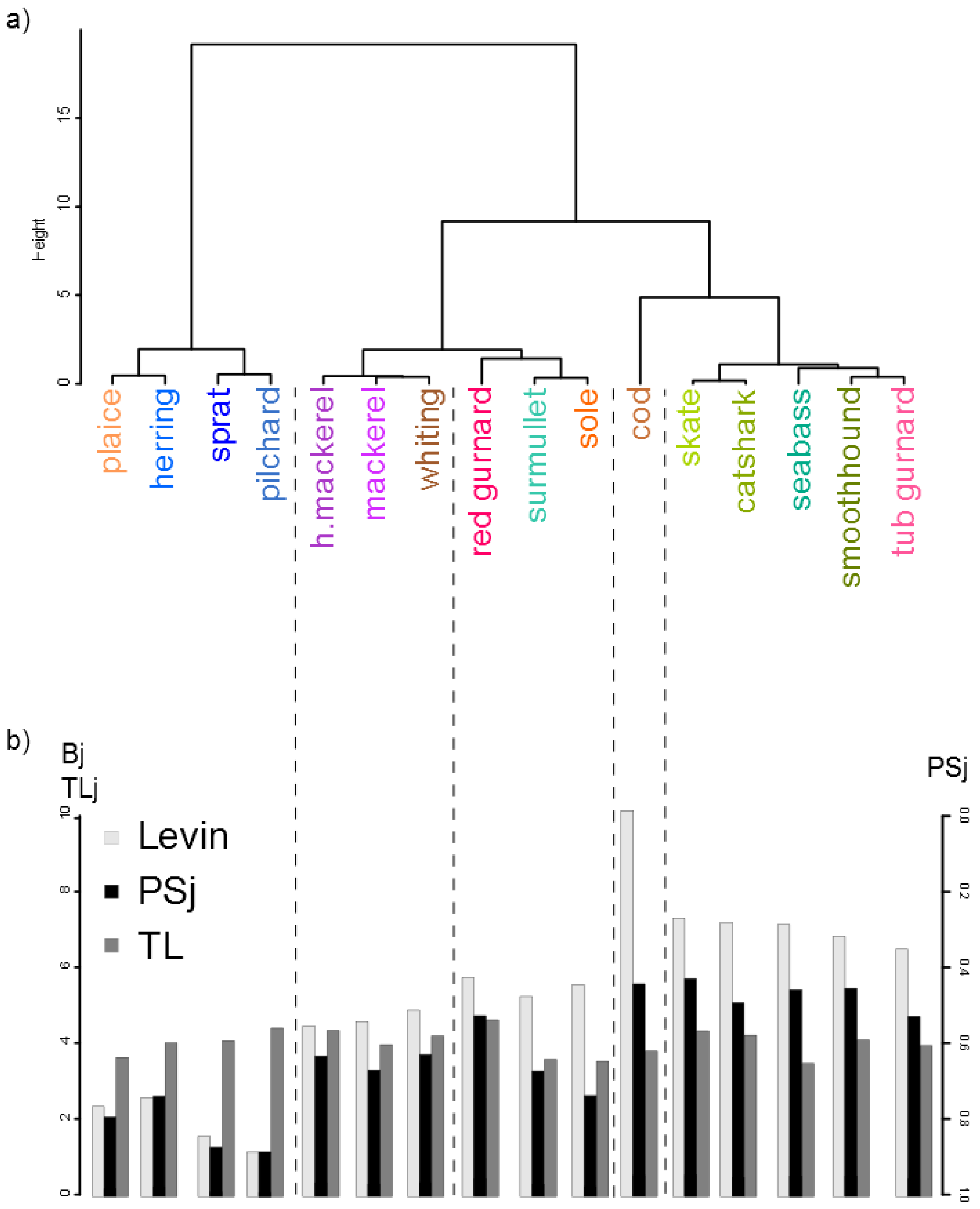

Figure III.3 : a) Hierarchical clustering of species trophic characteristics of focal fish species, namely Levin' index of trophic niche breadth (B_j), PS_j species trophic specialization, and TL_j species trophic level. b) Bar graph of dietary indices (B_j, PS_j and TL_j).

In the first branch plaice, herring, sprat and pilchard had the narrowest niche breadths (B_j) and correlatively the highest dietary specialization (lowest PS_j, **Fig. III.3 a, and b**). Then, horse mackerel, mackerel and whiting had very close values of PS_j (between 0.33 and 0.37) and similar medium niche breadths (**Fig. III.3 a, and b**). Red gurnard, surmullet and sole belonged to the same branch (and so exhibited similar characteristics), with medium but larger niche breadths, relatively high dietary specialization. Cod was separated from the last branch by its particularly high value of Levin's index of niche breadth (B_j = 10.2 **Fig. III.3 a, and b**). Finally, skate, catshark, seabass, smoothhound and tub gurnard followed a similar pattern, with relatively large niche breadths and medium specialization (PS_j around 0.5, **Fig. III.3 a, and b**).

III.4.2 Investigating the importance of spatial variation and ontogenetic diet shift

Full factorial db-RDAs found no significant explaining variables for 10 out of 16 focal fish species (**Table III.1**). After running three successive db-RDA, the 6 remaining species (herring, horse mackerel, surmullet, sole, skate and smoothhound), exhibited a significant variation in diet composition with size or with size and depth (**Table III.1**). It appeared that the critical size at which appeared ontogenetic diet shift (i.e. effect of size on diet variation), detected by MRT constrained by size, was 10 cm for herring, 10.5 cm for surmullet, 26 cm for horse mackerel, 25.5 cm for sole, 22 cm for skate and 53.5 cm for smoothhound. These 6 species were further split into two groups: "small" and "large" individuals, depending on if their sizes were above or below their respective critical size, for the metacommunity network computation (see **ESM III.1 & 3**). Within these six species, only three, namely horse mackerel, skate and smoothhound, exhibited an impact of both depth and size on individual diet composition. In particular, they had a significant effect of size in deeper waters (below 20 m), but not in shallow waters (above 20 m, **Table III.1**). Consequently, for these three species, those caught below 20 m were further split into two groups: "small" and "large" individuals, depending on if their sizes were above or below their respective critical size, for the "community below 20 m" network computation (see **ESM III.1 & 3**).

Table III.1: Results of full factorial db-RDA relating the effect of size and depth on individual diet composition in the metacommunity, and the effect of size alone in shallow waters (above 20 m) and in deep waters (below 20 m).). For each focal fish species, models were considered non significant (*ns*) when *P*-values were above 0.05. When significant, the remaining variable and its related *P*-Value, detected in the reduced model after stepwise selection, was given. (*P*-values < 0.05 *; *P*-values < 0.01 **; *P*-values < 0.001 ***). All *P*-values included a Bonferroni correction. NA = species considered as absent since no individuals were caught at depth.

Species	**metacommunity**	**community above 20 m**	**community below 20 m**
Plaice	*ns*	*ns*	*ns*
Herring	depth and size (***)	*ns*	*ns*
Sprat	NA	NA	*ns*
Pilchard	*ns*	*ns*	*ns*
Horse mackerel	size (***)	*ns*	size (***)
Mackerel	*ns*	*ns*	*ns*
Whiting	*ns*	*ns*	*ns*
Red gurnard	*ns*	*ns*	*ns*
Surmullet	size (***)	*ns*	*ns*
Sole	size (***)	*ns*	*ns*
Cod	*ns*	*ns*	*ns*
Skate	depth and size (***)	*ns*	size (***)
Catshark	NA	NA	*ns*
Seabass	*ns*	*ns*	*ns*
Smoothhound	NA	NA	size (***)
Tub gurnard	*ns*	*ns*	*ns*

III.4.3 Structure of the trophic network

The metacommunity trophic network exhibited six trophic compartments (**Fig. III.4 a**) characterised by their consumption of prey, which allowed the refining of trophic identities of species after their previous characterisation by trophic indices. Compartments were computed based on species' diets (p_{ij} see **ESM III.4**), including "small" and "large" individuals for species previously detected as exhibiting ontogenetic diet shifts (i.e. herring, horse mackerel, surmullet, sole, skate and smoothhound).

First, planktivorous species, namely: herring (small and large), sprat, small horse mackerel and pilchard that ate copepods and crustacean larvae (**Fig. III.4 a**). Then second, large horse mackerel, mackerel and whiting, characterised essentially by a consumption of fish, and so called piscivorous species. The third compartment, named as "demersal-piscivorous", was composed of seabass and tub gurnard, eating demersal fish prey (mainly dragonets). The larger compartment was composed of red gurnard, cod, catshark, skate (small and large) and smoothhound (small and large), and exhibited a wide diversity of prey categories (several crustacean, mainly crabs, and some cephalopods, **Fig. III.4 a**). This was then defined as the malacophagous compartment. The fourth compartment, which was defined as benthivorous, comprised of surmullet (small and large) and sole (small and large), whose preferential prey categories were amphipods and polychaetes (**Fig. III.4 a**). The fifth and last compartment was composed of a single species, namely plaice, with a high proportion of clams in its diet (**Fig. III.4 a**). Proportions of prey categories in diets of fish species were then considered as a quantification of trophic relationships' strength and then used to depict the metacommunity's trophic network (**Fig. III.4 b**). It appeared that the prey category of "other decapod" had a central localisation in the illustration of the metacommunity's trophic network. It was in fact, the only prey category that was present in all focal fish species' diets (see **ESM III.4**).

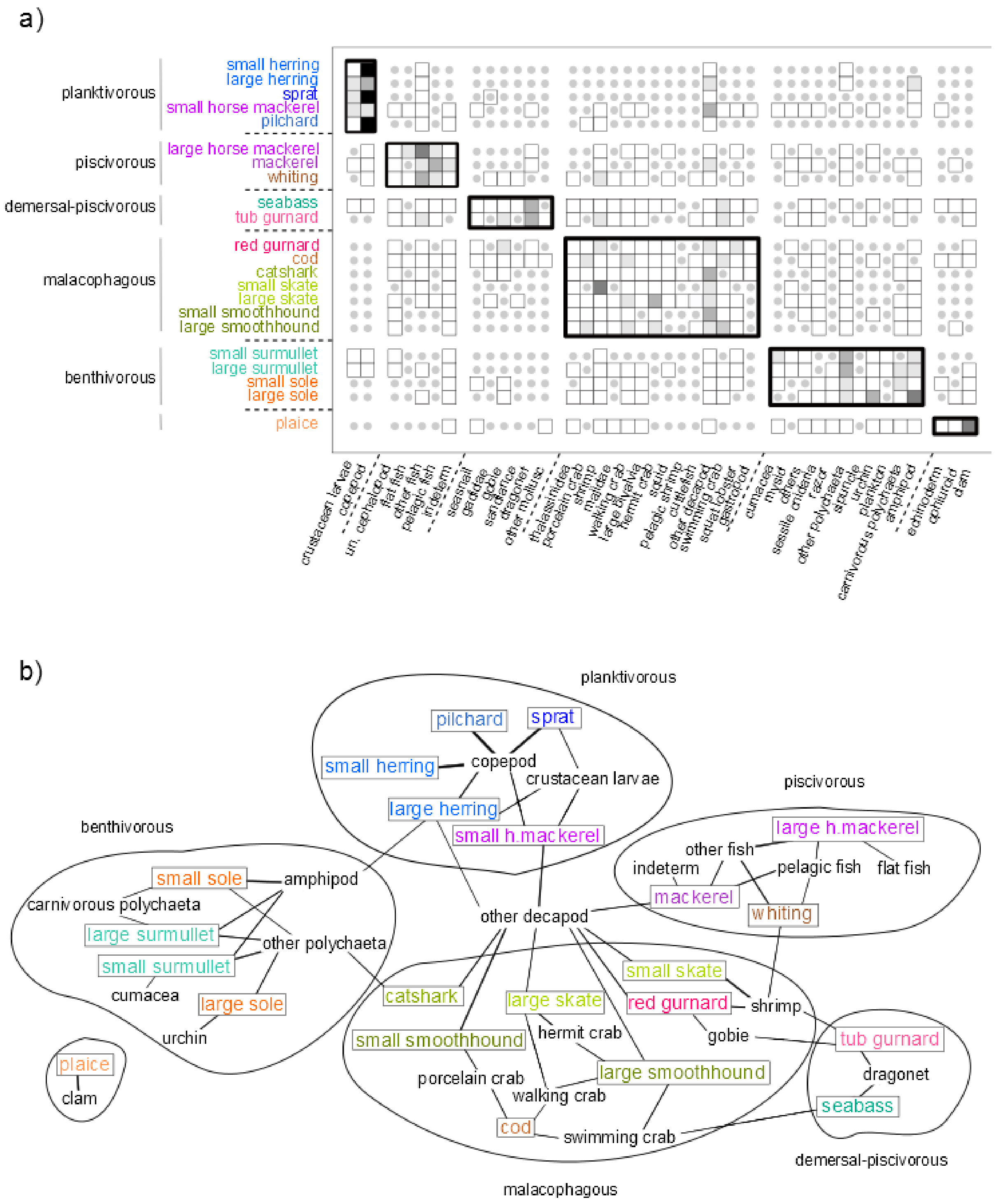

Figure III.4: a) compartmentalization of the metacommunity's trophic network. Each trophic compartment is characterised by focal fish species (on the left) and their prey categories (at the bottom). b) Illustration of the metacommunity trophic network. Edge widths are proportional to trophic relationships' strength (considered as the proportion of prey category in the diet of fish species, p_{ij}) and compartments described before are circled. For readability purposes, only prey categories counting for more than 10% of fish diet are represented.

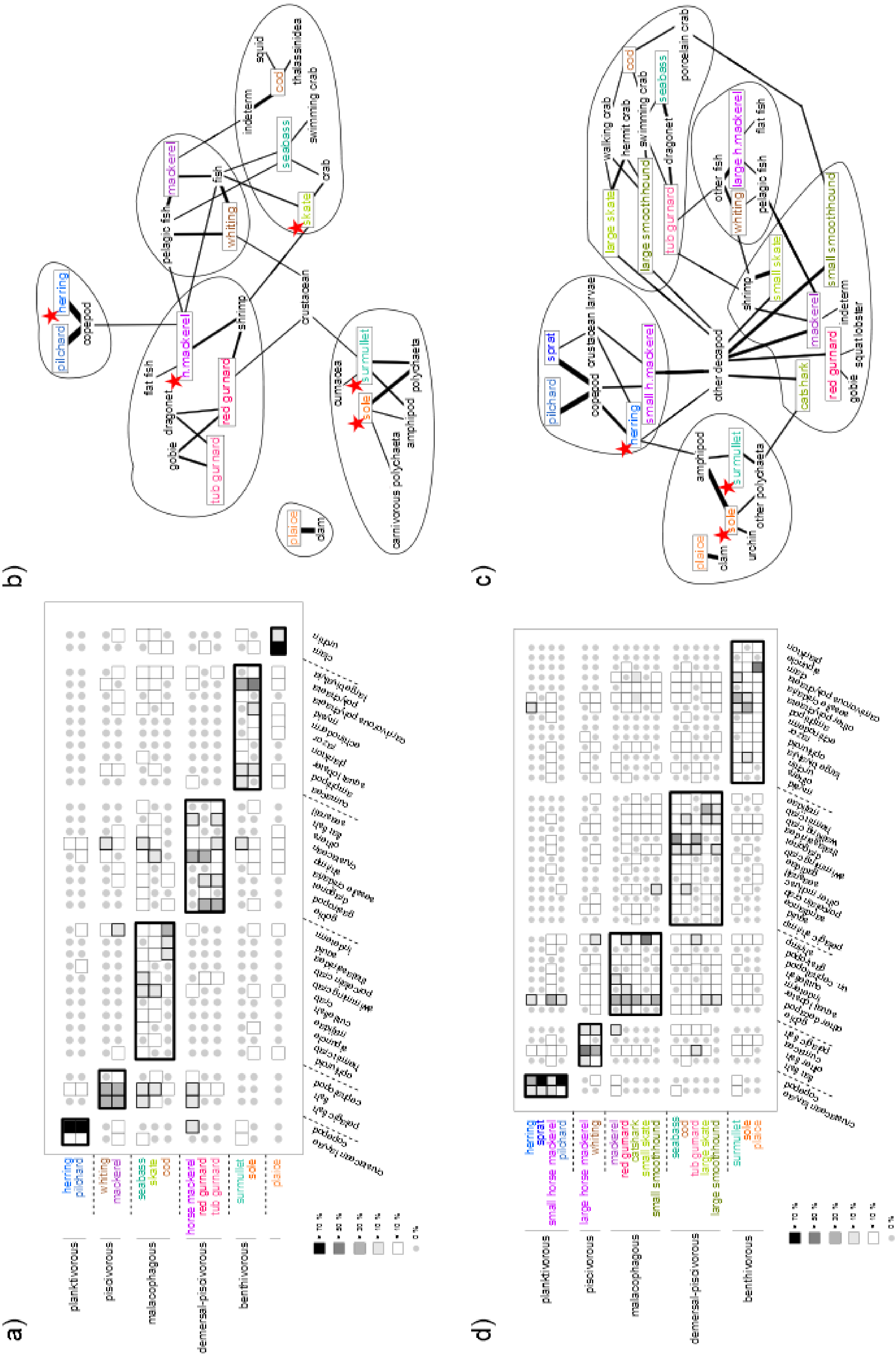
a)
b)
c)
d)
planktivorous
piscivorous
malacophagous
demersal-piscivorous
benthivorous
herring
pilchard
whiting
mackerel
seabass
skate
cod
horse mackerel
red gurnard
tub gurnard
surmullet
sole
plaice
70 %
50 %
30 %
10 %
10 %
0 %
copepod
pelagic fish
fish
crustacean
shrimp
dragonet
gobie
flat fish
h.mackerel
indeterm
squid
thalassinidea
swimming crab
crab
cumacea
amphipod
polychaeta
carnivorous polychaeta
clam
sprat
crustacean larvae
small h.mackerel
other decapod
catshark
squat lobster
large skate
walking crab
hermit crab
large smoothhound
small smoothhound
small skate
porcelain crab
other fish
large h.mackerel
urchin
other polychaeta
small horse mackerel
large horse mackerel

Figure III.5: Compartmentalization and illustration of trophic networks above and below 20 m. a) compartmentalization of the shallow trophic network, i.e. above 20 m. Each trophic compartment is characterised by focal fish species (on the left) and their prey categories (at the bottom). b) Illustration of the shallow trophic network, i.e. above 20 m. c) compartmentalization of the deeper trophic network, i.e. below 20 m. Each trophic compartment is characterised by focal fish species (on the left) and their prey categories (at the bottom). d) Illustration of the deeper trophic network, i.e. below 20 m. Edge widths are proportional to trophic relationships' strength (considered as the proportion of prey category in the diet) and compartments described before are circled. Stars mean that for this focal fish species, both small and large individuals were gathered. For readability purposes, only prey categories counting for more than 10% of fish diet are represented.

Since a change in community composition was detected at a depth of 20 m, individuals of each species were split into those caught above 20 m and those caught below 20 m. Species caught that exhibited an ontogenetic diet shift below 20 m (horse mackerel, smoothhound and skate) were split into small and large groups. Then, as previously, compartmentalization was computed and related networks were depicted (**Fig. III.5**).

The trophic network above 20 m, where smoothhound, catshark and sprat were absent and where no species exhibited a significant ontogenetic diet shift, contained six different trophic compartments (**Fig. III.5 a and b**). Herring and pilchard still belonged to the compartment of planktivorous species, like mackerel and whiting, which still made up the piscivorous one (**Fig. III.5 a and b**). The benthivorous compartment comprised of surmullet and sole. Above 20 m, species from initial malacophagous and demersal-piscivorous compartments were redistributed. Firstly, horse mackerel, red gurnard and tub gurnard were grouped and characterised by diverse prey categories, comprising of several demersal fish such as dragonet and goby, and crustacean such as shrimp and mollusc (sea snail and other gastropod, **Fig. III.5 a and b**). Then, cod, seabass and skate were gathered by their consumption of several crustacean prey categories (mainly crab and swimming crab). Finally, plaice was again alone and characterised by the same prey category, i.e. clam (**Fig. III.5 a and b**).

Below 20 m, where all species were present and where horse mackerel, smoothhound and skate were split into small and large individuals as they exhibited ontogenetic diet shift; the trophic network had five compartments (**Fig. III.5 c and d**). The planktivorous compartment comprised of the same species as at the level of the metacommunity, i.e. herring, sprat, pilchard and small horse mackerel. The piscivorous compartment was now composed of large horse mackerel and whiting. Two demersal compartments were created (**Fig. III.5 c and d**) resulting from a reorganisation of demersal-piscivorous and malacophagous compartments. Firstly, mackerel, red gurnard, catshark, small skate and small smoothhound were gathered and characterised by their relatively high consumption of crustaceans, but also, to a lesser extent, cephalopods. Secondly, seabass, cod, tub gurnard, large skate and large smoothhound exhibited preferential prey categories with several crustacean types (mainly swimming crab and shrimp), and different fish groups (essentially goby, dragonet, and other fish). Plaice was no longer alone, and belonged to the benthivorous compartment together with surmullet and sole, eating mainly polychaetes (**Fig. III.5 c and d**).

The network metrics highlighted the marginal structure of the network above 20 m (**Table III.2**). For linkage density D, connectance C, nestedness N and modularity M, the metacommunity network and the network below 20 m were relatively similar (D = 6.44 to 5.92 respectively, C = 0.102 and 0.097 respectively, Nestedness and Modularity around 0.5,

Table III.2). The network above 20 m, where three fish species were absent (i.e. smoothhound, catshark and sprat), was a clear exception for all metrics with lowest values for linkage density (D = 3.04), connectance (C = 0.056) and nestedness (N = 0.31), and the highest value of modularity (0.60, **Table III.2**).

Table III.2: Networks' metrics calculated to describe topologies of trophic networks. For the three types of trophic networks, i.e. metacommunity, above 20 m and below 20 m, linkage density D (number of link L per species S, $D = L/S$), connectance C (proportion of link realised compared to all potential links, $C = L/S^2$), nestedness N (measures to what extent interaction by specialist are nested within generalists' interactions) and modularity M (compartmentalization of the network) were collected.

Type of network	**D**	**C**	**N**	**M**
Metacommunity	6.44	0.102	0.45	0.52
Community above 20 m	3.04	0.056	0.31	0.60
Community below 20 m	5.92	0.097	0.44	0.50

III.5 Discussion

This study allowed us to describe and depict the compartmentalized structure of a metacommunity trophic network. It highlighted the minor importance of ontogenetic diet shift, at least when larvae were excluded, on compartmentalization and trophic network topology; whereas the main implication of spatial variation on properties of the trophic network's structure was determined. Two sub-networks within the metacommunity were described, from a coastal and shallow community to an offshore and deeper community.

III.5.1 A wide diversity of trophic identities in the fish metacommunity

The metacommunity trophic network exhibited five trophic compartments wherein fish species had relatively similar trophic identities that may be related to their prey preferences and habitat characteristics. Most of the compartments were consistent with previous studies on other marine ecosystem (North sea, Christensen 1995; Greenstreet *et al.* 1997). The planktivorous compartment consists of highly specialized fish species, with a similar lifestyle (i.e. living in pelagic school, Pettorelli *et al.* 2011). Other specialized species, to a lesser extent however, were found in the benthivorous compartment (surmullet and sole), and in the piscivorous compartment (large horse mackerel, mackerel and whiting). Between these pelagic and benthic compartments, the demersal component of the trophic network included two compartments: the demersal-piscivorous and the malacophagous, which included a high richness of species, both in term of fish species and prey categories. It sustained a larger diversity of fish species, mainly exhibiting omnivorous trophic identities (e.g. sharks, gurnards and cod).

Two species exhibited particular characteristics in our assemblage. Firstly, plaice, separated from other compartments and which appeared as an original species. Its trophic characteristics (both diet and niche) revealed a trophic identity of a benthic specialist (narrow niche breadth and high specialization), but it had contrasted trophic relationships (particular prey categories like clam) compared to other benthic fish. This trophic complementarity (the consumption of different food resources compared to others, Loreau *et al.* 2001; Poisot *et al.* 2013) points out that the plaice, in our metacommunity, has a high level of trophic originality. This last point is important as it highlights the particular importance of some species, i.e. trophically original species, in adding new trophic relationships in the food web.

Secondly, horse mackerel appeared as a transitional species between planktivorous and piscivorous compartments. It was categorised in the pelagic compartment when small; while having a more piscivorous diet when it grew. Horse mackerel is a species that exhibits a switch in habitat and lifestyle, being pelagic and living in schools when young, and becoming more demersal when adult. It is a good example of a species that can belong to different trophic compartments and thus can assume different functional roles during its life span (Link 2002). It also highlights a clear topology of a trophic metacommunity where, at the large spatial scale, pelagic and the benthic communities are distinct, but connected by species like horse mackerel.

Another notable result was trophic level. Trophic levels of piscivorous species were not the highest across our fish species, implying that they could not be considered as top predators despite their piscivorous diet. An explanation would be that many invertebrates found in our prey categories (like swimming crabs) and consumed by other species from demersal compartments, are known to feed on discards and thus may as high have trophic level as prey-fish (Gislason 1994; Gislason & Sinclair 2000; Groenewold & Fonds 2000). Discards have already been described as a new source of food for many demersal fish, which tend to change opportunistically their diets and thus their trophic relationships. Consequently, fishing, by changing trophic relationships, has an important impact on food chains and food webs (Kaiser & Spencer 1994; Jennings & Kaiser 1998; Gislason & Sinclair 2000; Groenewold & Fonds 2000).

III.5.2 The small importance of ontogeny

It is generally admitted that body size determines the prey range of a predator, and consequently is a relevant proxy of diet and trophic level (Webb 1984; Wainwright & Richard 1995; Scharf *et al.* 2000). Contrary to this assumption, body size had an effect on diet for only six out of the 16 focal fish species, and even more, they belonged to the same trophic compartment in the metacommunity network, whether for small or large individuals. This may be explained by the fact that only secondary prey items change with size, whereas the main set of prey stay the same across life stages. In fact, ontogenetic shift of the trophic niche concerned only one species in the fish community - horse mackerel, which changed compartments between small and large individuals. Ontogenetic niche shift in fish is generally related to ontogenetic habitat shift and affects the transition between pelagic larvae and well developed-individuals (metamorphosis). However, our study did not focus on pelagic larvae, but on juveniles' and adults' trophic relationships. Nevertheless, this marginality of ontogenic niche shift in fish species (larvae not included) is consistent with previous studies on sharks (Pauly *et al.* 1998b; Cortes 1999) and on the fish community of the North Sea (Jennings *et al.* 2001). It is reasonable to think then that the general absence of size effect on diet variation may have resulted from (i) a lack of prey diversity in a semi-enclosed continental shelf like the English Channel, or (ii) an unsuspected trend, for fish species, to select same main prey items during their life span (dietary preference). Beyond these hypotheses, an important point is that ontogeny has little influence on compartment organization, and thus on trophic network structure. Following Jennings *et al.* (2002) who raised the question of the relevance of size-based metrics and models to describe trophic networks in the North sea fish community, it may be possible that same size-based approach would not be relevant for shallow semi-enclosed ecosystems such as the English Channel.

Across our analyses, the main determinant of trophic network structure was the spatial variation of community's composition, highlighting a shallow (above 20 m) and a deeper (below 20 m) community. An important point is that, since the size ranges of these individual fish species greatly overlapped between these two communities, there is no clear ontogenetic habitat shift that would imply an ontogenetic diet shift (e.g. coastal small individuals and offshore large individuals). On the contrary, the spatial variation of the structure of the trophic network in fact came from differences in species' identities related to differences in community composition.

III.5.3 The main impact of community composition

The shallow trophic sub-network (above 20 m) had a marginal structure compared to others. Firstly, its fish community held less species (sprat, smoothhound and catshark were absent), but had six trophic compartments (highest value of modularity M = 0.60, **Table III.2**), resulting from the reorganization of the malacophagous and demersal-piscivorous compartments into two separated, but still demersal compartments. Secondly, its density of connection (D), connectance (C), and nestedness (N) were particularly low (**Table III.2**). All these characteristics depict a community relatively poor in terms of trophic relationships, but where interactions are strong, and the presence of a trophic complementarity between compartments. Thirdly, there was no species that exhibited an ontogenetic diet shift in these shallow waters. With this particular topology, the shallow community appeared as an example of the main importance of species trophic identity for the structure of a trophic network. Many authors (Loreau 2000; Loreau *et al.* 2001; Hooper *et al.* 2005; Carey & Wahl 2011; Narwani & Mazumder 2012) have highlighted that species identity and complementarity, rather than species richness, do have effects on trophic structure, since some species make a unique contribution to some processes (here, plaice). Our results were consistent with this hypothesis and, since trophic interactions affect ecosystems' functioning (Petchey *et al.* 2004), it may be reasonable to hypothesise that the shallow community has a different energetic flows dynamic from the deeper one (below 20 m, Duffy *et al.* 2007; Poisot *et al.* 2013).

When looking at the topology of the deeper sub-network, it appeared to have numerous trophic interactions (linkage density and connectance), and an overlap between specialist and generalist food resources (nestedness), illustrated by the benthivorous compartment that included plaice. Interestingly, the deeper community was the one where species exhibited ontogenetic diet shifts, if any. Horse mackerel presented the same pattern as in the metacommunity trophic network, i.e. small individuals in the planktivorous compartment and large individuals in the piscivorous compartment. The two other species that exhibited an ontogenetic diet shift (catshark and smoothhound) where split between the two demersal compartments, which in fact differed mainly by their secondary prey categories (cephalopod VS demersal fish).

It is important here to take a look at the trophic identity of the three new species that were absent in the shallow community. Except sprat, the two new species were omnivorous shark (smallspotted catshark and smoothhound). Omnivory is the trend for an organism to feed on numerous and various prey items. Consequently, omnivorous organisms are implicated in many trophic relationships and thus increase the density of trophic links within a trophic network. Following this idea, it may be hypothesised that trophic identity of species, rather than their diversity, matters in the structure of trophic networks (Fagan 1997; Bascompte & Melian 2005).

One major point to take from this study is that, accordingly to our hypothesis, the structure of the metacommunity's trophic network exhibited a spatially-based disparity due to changes in species' interactions. Changes in species composition from coastal community to offshore community is probably mainly due to particularly sedentary species like polychaetes, bivalves, and other prey items consumed by fish species. They create a mosaic of local communities (or patches) within trophic relationships that may be different, creating the sub-networks highlighted in our analyses. However, community's sub-networks are connected to each other by the movement of predators like fish, since they tend to have wide home ranges concerning the whole eastern English Channel. The implication of such a hierarchical organisation, i.e. a metacommunity trophic network comprising of spatial sub-networks related to local community composition, and connected by higher-order mobile predators, within each appeared highly connected species assemblage (compartments), is a central question in ecology since it may impact on the stability of a food web (Leibold *et al.* 2004; Rooney *et al.* 2006, 2008; Pillai *et al.* 2011).

III.5.4 Limits and perspectives

Using stomach contents from one collection has only really allowed us to describe a snapshot of trophic relationships, but such a large dataset appears as an efficient tool to investigate determinants of the structure of the trophic network. Unfortunately, we were not able to describe temporal variation of trophic relationships (and of trophic network structure), but it is highly probable that mobile species, such as fish, seasonally migrate between shallow and deep waters, and may create spatial flows between communities (McCann *et al.* 2005). The discrimination of the eastern English Channel at a depth of 20 m based on its species composition was a way to investigate spatial impact on trophic network structure, but it is important here to remind ourselves that, in fact, changes in species composition are generally gradual and consequently boundaries of sub-networks and communities are blurred.

However, to our best knowledge, this study has described here for the first time a semi-enclosed sea, and this deserves more investigation in order to determine if it is a cause or a consequence of the long-term exploitation of the area (Halpern *et al.* 2008).The English Channel has been intensively exploited for decades (Christensen *et al.* 2003; Thurstan *et al.* 2010) and Bascompte *et al.* (2005) reminded us that fishing has had a stronger impact on community composition than expected, because of its asymmetrical removal of species. By inducing a non-random loss of species, fishing may change the structure of the community (loss of top predators, change in compartment organization). It may thus destabilize and simplify the structure of a trophic network. Consequently, it would be interesting to detect the impact of fishing with long-term data, and/or to simulate extinction in this trophic network to assess its potential stability or fragility facing fish stocks collapse.

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III.6 References

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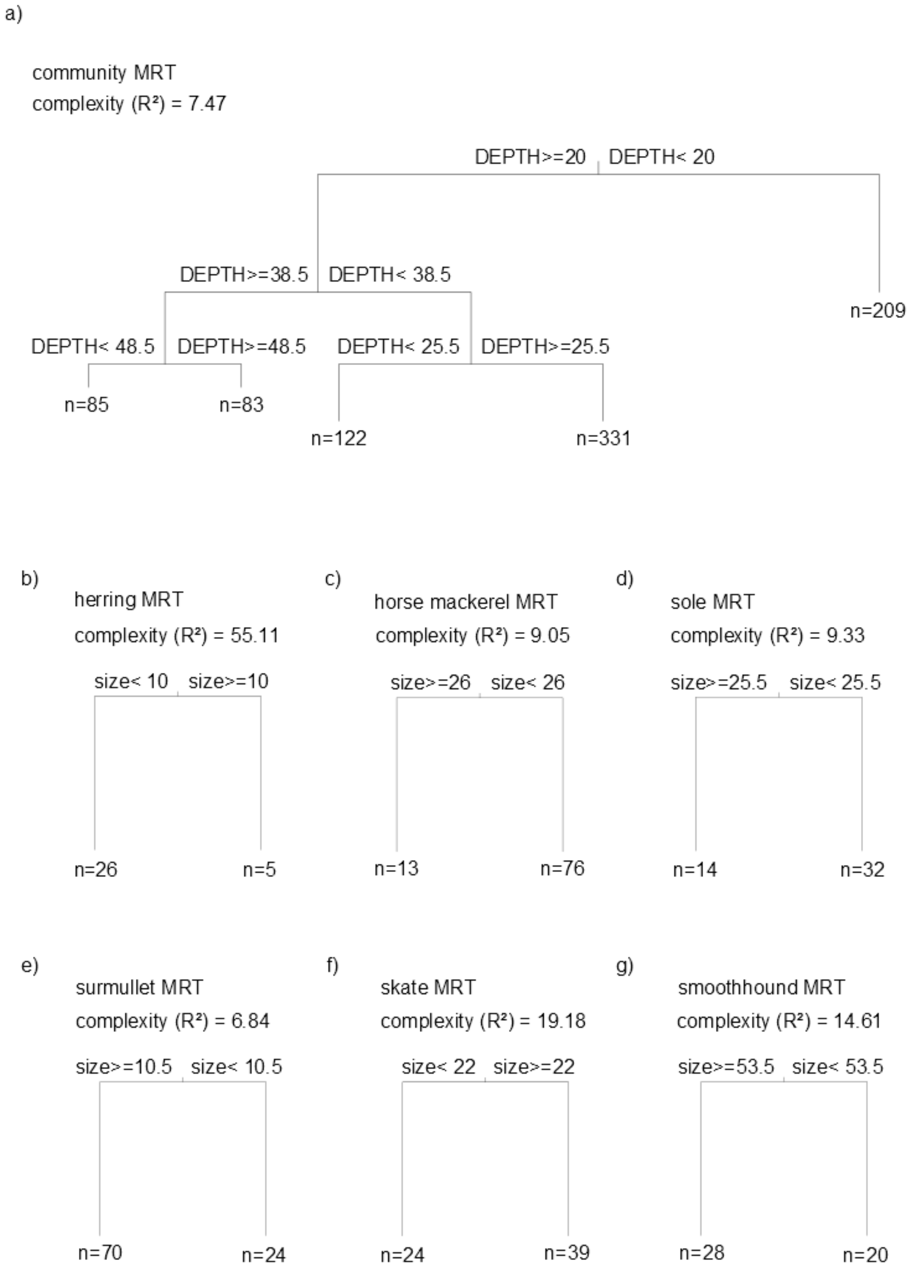
III.7 Supplementary materials

ESM III.1: Multivariate Regression Tree and related complexity (R^2). a) MRT on vertebrates and invertebrates species' presence-absence data recorded during CGFS 2009 under the constraints of depth. b) MRT of herring on individual diet composition constrained by size. c) MRT of horse mackerel on individual diet composition constrained by size. d) MRT of sole on individual diet composition constrained by size. e) MRT of surmullet on individual diet composition constrained by size. f) MRT of skate on individual diet composition constrained by size. g) MRT of smoothhound on individual diet composition constrained by size.



ESM III.2: Values of dietary indices for fish species based on their diet (P_{ij}) and their scaled values in brackets. Levin (B_j) is a classical index for trophic niche breadth, PS_j is a quantification of species trophic specialization (low PS_j meaning high dietary specialization and the reverse), and TL_j is the species trophic level.

Species	B_j	PS_j	TL_i
Plaice	2.38 (-1.19)	0.21 (-1.11)	3.68 (-1.12)
Herring	2.62 (-1.09)	0.26 (-0.76)	4.07 (0.02)
Sprat	1.59 (-1.51)	0.13 (-1.63)	4.12 (0.16)
Pilchard	1.18 (-1.68)	0.12 (-1.71)	4.45 (1.15)
Horse mackerel	4.51 (-0.30)	0.37 (-0.07)	4.40 (0.99)
Mackerel	4.62 (-0.26)	0.33 (-0.30)	4.01 (-0.15)
Whiting	4.92 (-0.13)	0.37 (-0.04)	4.25 (0.55)
Red gurnard	5.78 (0.22)	0.48 (0.62)	4.67 (1.79)
Surmullet	5.29 (0.02)	0.33 (-0.32)	3.63 (-1.26)
Sole	5.60 (0.15)	0.27 (-0.75)	3.58 (-1.42)
Cod	10.20 (2.05)	0.56 (1.17)	3.84 (-0.64)
Skate	7.35 (0.87)	0.58 (1.27)	4.38 (0.93)
Catshark	7.25 (0.82)	0.51 (0.85)	4.26 (0.60)
Seabass	7.19 (0.81)	0.55 (1.08)	3.51 (-1.60)
Smoothhound	6.88 (0.68)	0.55 (1.10)	4.14 (0.22)
Tub gurnard	6.53 (0.53)	0.48 (0.62)	3.98 (-0.23)

ESM III.3: Table of effectives and size ranges (in cm) in brackets for fish species under study, across the whole eastern English Channel, in shallow waters (above 20 m) and in deep waters (below 20 m). NA = species considered as absent since no individuals were caught at depth. * and *** indicates that the t-test between mean size above and below 20 m is significant, i.e. P-value < 0.05 and P-value < 0.001, respectively.

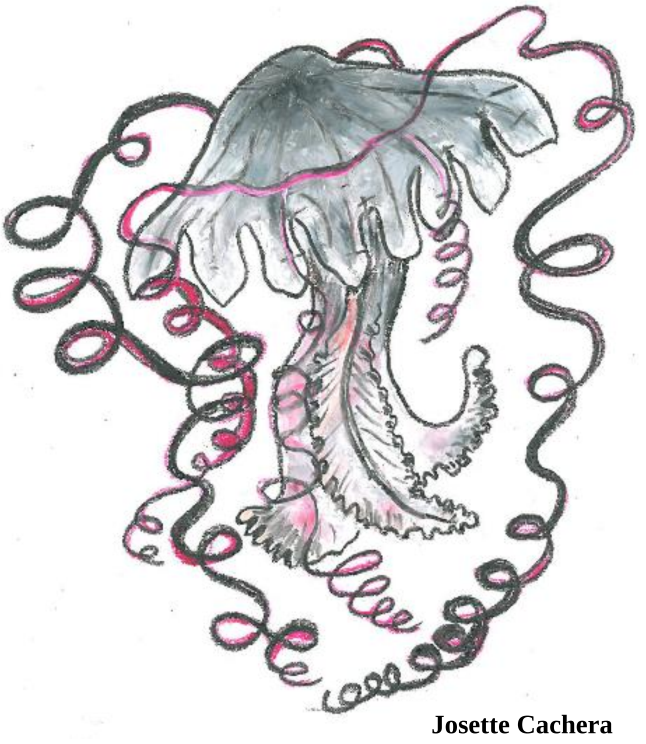
Species	**Whole community**	**Above 20 m**	**Below 20 m**
Herring	31 (6-25)	26 (6-9)	5 (11-25)
Sprat	24 (7-14)	NA	24 (7-14)
Pilchard	30 (20-31)	14 (22-31)*	16 (20-30)*
Horse mackerel	89 (8-39)	8 (11-36)	81 (8-39)
Mackerel	54 (7-29)	35 (7-29)	19 (8-27)
Whiting	56 (7-41)	9 (15-27)	45 (7-41)
Seabass	76 (26-73)	30 (26-49)***	46 (31-73)***
Red gurnard	42 (20-31)	4 (22-31)	38 (20-30)
Skate	63 (11-42)	11 (16-39)	52 (11-42)
Cod	40 (35-76)	4 (54-62)	36 (35-76)
Smoothhound	48 (33-89)	NA	48 (33-89)
Tub gurnard	48 (16-44)	24 (16-30)****	24 (19-44)***
Surmullet	94 (6-33)	13 (6-32)	81 (7-33)
Sole	46 (10-38)	14 (10-29)***	31 (10-38)***
Catshark	38 (20-64)	NA	38 (20-64)
Plaice	69 (9-43)	17 (9-33)	52 (18-43)

ESM III.4: Detailed diet of predatory species expressed as proportion of geometric mean (p_{ij}).

Prey categories	red gurnard	herring	seabass	cod	whiting	surmullet	smoothhound	plaice	skate	pilchard	mackerel	catshark	sole	sprat	horse mackerel	tub gurnard
Amphipod	0.01	0.10	0	0	0	0.26	0	0	0	0	0	0.01	0.33	0.01	0.04	0
Carnivorous Polychaete	0	0	0.03	0.03	0	0.09	0.01	0.06	0	0	0	0.09	0.09	0	0	0
cephalopod	0	0	0	0.01	0	0	0.01	0	0.01	0	0.04	0.04	0	0	0	0.01
Clam	0	0	0	0.01	0	0.01	0	0.64	0	0	0	0	0.01	0	0	0
Copepod	0	0.58	0	0	0.01	0	0	0	0	0.92	0.03	0	0	0.78	0.23	0
Crab	0.01	0	0.08	0.12	0	0.01	0.13	0.01	0.11	0	0	0.02	0	0	0	0.03
Crustacean	0.28	0.10	0.05	0.03	0.07	0.07	0.26	0	0.18	0.04	0.20	0.29	0.01	0.02	0.36	0.10
Crustacean larvae	0	0.13	0	0	0	0	0	0	0	0.02	0	0	0	0.15	0.17	0
Cumacea	0	0	0	0	0	0.01	0	0	0	0	0	0	0.01	0	0.01	0
Cuttlefish	0	0	0	0	0	0	0	0	0	0	0	0.02	0	0	0	0.00
Dragonet	0.03	0	0.30	0.03	0	0	0	0	0	0	0.04	0	0	0	0.01	0.29
Echinoderm	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fish	0.06	0.04	0.07	0.06	0.38	0	0	0	0.04	0.02	0.21	0.05	0	0.04	0.10	0.10
Flat fish	0	0	0	0.01	0.01	0	0	0	0	0	0	0	0	0	0.02	0.03
Gadidae	0	0	0.05	0.04	0.02	0	0	0	0.01	0	0	0.01	0	0	0	0
Gastropod	0	0	0	0	0	0	0	0	0	0	0	0.02	0	0	0	0
Gobie	0.15	0	0.01	0.02	0.06	0	0	0	0	0	0	0.01	0	0	0	0.14
Hermit crab	0.01	0	0	0	0	0	0.11	0	0.24	0	0	0.06	0	0	0	0
indeterm	0	0	0.01	0.03	0.01	0.01	0.02	0.02	0.03	0	0.14	0.03	0	0	0	0
Large bivalve	0	0	0	0.03	0	0.02	0	0.04	0.01	0	0	0.06	0.01	0	0	0.02
Majidae	0	0	0.01	0.01	0	0.00	0.03	0.01	0.01	0	0	0.03	0	0	0	0
Mollusc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01
mysid	0	0	0	0	0	0.04	0	0	0	0	0	0	0	0	0	0
Ophiuroid	0	0	0.01	0.05	0	0	0	0.04	0	0	0	0	0.02	0	0	0
others	0	0	0	0	0	0.02	0	0	0.01	0	0	0	0	0	0	0
Pelagic fish	0	0	0.05	0.04	0.13	0	0	0	0.02	0	0.33	0	0	0	0.03	0.01
pelagic_shrimp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plankton	0	0	0	0	0	0.00	0	0	0	0	0	0	0	0	0	0

Polychaete	0	0.04	0.02	0	0.06	0.32	0.01	0.04	0	0	0	0.17	0.17	0	0	0
Porcelain crab	0.02	0	0.02	0.21	0	0	0.09	0	0	0	0	0.02	0.01	0	0	0
Razor	0	0	0	0	0	0.01	0	0.03	0	0	0	0	0.02	0	0	0
Sandlance	0	0	0.05	0.03	0.03	0	0	0	0.01	0	0	0	0	0	0	0
Seasnail	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0
Sessile cnidaria	0	0	0	0	0	0	0	0.02	0	0	0	0	0.04	0	0	0.01
Shrimp	0.23	0	0.03	0.03	0.17	0.06	0.05	0.00	0.15	0	0	0.03	0.04	0	0.03	0.13
Sipuncle	0	0	0.01	0	0	0	0	0	0	0	0	0	0.02	0	0	0
Squat lobster	0.10	0	0	0.02	0	0.04	0.05	0	0.01	0	0	0.01	0.01	0	0	0
Squid	0	0	0	0.01	0	0	0	0	0.05	0	0	0.01	0	0	0	0
Swimming crab	0.06	0	0.14	0.16	0.01	0.01	0.17	0	0.07	0	0	0	0.01	0	0	0.10
Thalassinidae	0.02	0	0.04	0.01	0.05	0.01	0.05	0.01	0.04	0	0	0.04	0.03	0	0	0
Urchin	0	0	0	0	0	0	0	0.07	0	0	0	0	0.16	0	0	0

Chapter IV Competitive, functional and specific determinants of the Niche Variation Hypothesis in a fish community



Josette Cachera

IV.1 Abstract

The Niche Variation Hypothesis (NVH) states that a wider ecological niche would permit greater individual phenotypic or niche variation. When focusing on trophic niche, species niche breadth and individual diet variation are expected to be determined by the balance between inter-specific competition for food resources, which favours diet convergence among conspecifics and niche contraction, and intra-specific trophic competition, which promotes diet diversification between conspecifics and niche expansion. However, the NVH was very seldom tested on trophic niche nor was it across species within a community, most previous studies comparing several populations of the same species. Besides competition, a species' trophic niche may depend on its functional identity that may constrain its ecological niche and conspecifics diet variation may take several patterns depending on sources of variation. Using a database of individual stomach contents belonging to sixteen fish species from the eastern English Channel community, the NVH was tested across species within the community and its potential determinants at the species-level, i.e. competitive pressure and functional identity, and at the individual-level, i.e. sex, maturity stage, body size and habitat, were investigated. The NVH, i.e. the positive correlation between trophic niche breadth and individual diet variation, was successfully supported at various levels of organization, i.e. across species within the community but also between and within functional groups, thus suggesting that functional identity partly constrains species niche and individual variation but that taxonomic identity within functional groups also matters. Diet overlap between species, a proxy of inter-specific competition, was not related to species trophic niche breadth nor to individual diet variation, possibly because of the absence of current competition resulting either from sufficiently abundant food resources or from the fact that species evolved to forage on most abundant prey items in order to relax past competition pressure. Finally, several patterns of conspecifics diet variation were detected and explained, for some species, by differences in size or habitat. The respective contributions of functional identity and current versus past competition to the NVH should be further investigated using community level approaches.

Keywords: functional group, competition, trophic niche, individual variation, diet, semi-enclosed marine area.

IV.2 Introduction

Intra- and inter-specific variation in ecological niche affects intra- and inter-specific interactions, influences population and community dynamics, determines species coexistence and community structure, and is a driver of evolution (Araùjo *et al.* 2011). It is thus a main challenge to identify forces that imply variation, whether it is among species or among conspecifics. The "Niche Variation Hypothesis" (NVH) proposed by Van Valen (1965) states that wider ecological niches would permit greater phenotypic variation among conspecifics (individual variation). Since then, competition was hypothesised to be at the origin of species ecological niche breadth and related variation among conspecifics.

Focusing on the trophic dimension of the ecological niche (trophic niche), strong intra-specific competition for food resources is expected to promote species niche expansion as individuals tend to diversify their diet in order to reduce interactions with conspecifics (Bolnick *et al.* 2003, 2010; Svanbäck & Persson 2004; Svanbäck & Bolnick 2007; Tinker *et al.* 2012). At the same time, strong inter-specific competition is supposed to induce species niche contraction and force individuals to forage on a few prey items in order to mitigate interactions with other species. Inter-specific competition also favours trophic niche diversification across species according to the principles of competitive exclusion and character displacement (Schluter 1996; Svanbäck *et al.* 2008). Consequently, species trophic niche position, breadth and associated individual diet variation should depend on the balance between intra- and inter-specific trophic competitions (referred to as competitive balance thereafter). More precisely, while a positive correlation between trophic niche breadth and individual variation is primarily expected from the NVH, negative relationships between inter-specific competitive pressures and both trophic niche breadth and individual variation are also predicted. However, observed relationships between competitive pressures and trophic niche organisation (position, breadth and individual variation) may differ according to whether resources are limiting or not, since, by definition, competition only takes place when resources are limiting.

Surprisingly, the NVH was tested on trophic niche only once (Bolnick *et al.* 2007). It was investigated for colour polymorphism between species of raptors, owls and nightjars (Galeotti & Rubolini 2004), for skull and canine shapes considered as surrogates for size and feeding niche, respectively, in terrestrial carnivore (Meiri *et al.* 2005), for genetic variation used as an indicator of phenotypic variation in marine fishes (Somero & Soulé 1974). But Bolnick *et al.* (2007) were the only ones who investigated the NVH applied to trophic niche by comparing the niches of different populations within 5 different taxa including fish, frogs, lizards and whelk, using dietary data. The NVH was successfully supported in all 5 taxa, trophic niche breadth increasing with the level of individual diet variation. However, this study did not provide the opportunity to test the implication of competition, and more precisely of the competitive balance as it was based on comparing different populations of the same species across ecosystems. One way to assess the involvement of the competitive balance for trophic resources in the NVH would be to compare the trophic niches of different species from the same community potentially sharing the same food resources. This would mean increasing the scope of the NVH in terms of level of organization by investigating whether it holds between species within a community and not only between populations, and thus between communities, within a single species.

One important aspect of the trophic niche and its variation is related to the precise pattern of individual occupation of the species trophic niche. A species considered as a trophic specialist, i.e. using only a subset of available food resources, and thus having a narrow niche should be composed of individuals using the same subset of food resources, thus exhibiting low level of individual diet variation. Conversely, a species considered as a trophic generalist, i.e. foraging on a large diversity of available food resources, has a broad trophic niche and is expected to comprise individuals using a wide variety of food items (Bolnick *et al.* 2003; Araùjo *et al.* 2011). However, individuals as a whole may use a wide variety of food items according to different patterns. The trophic niche of a generalist species can indeed be occupied by (i) specialist individuals, each of which uses a different subset of the food resources used by the species as a whole, (ii) generalist individuals, all of which use the same food resources as the species as a whole, (iii) a combination of generalists and specialists, or (iv) several specialized groups of individuals (Bolnick *et al.* 2003, 2007; Svanbäck & Persson 2004; Araùjo *et al.* 2008, 2010, 2011; Svanbäck *et al.* 2011) Therefore, a broad trophic niche may house a gradient from large to weak individual diet variation (patterns (i), (iv), (iii), and (ii)). It is thus crucial to account for patterns of individual diet variation in a trophically-based test of the NVH.

Beyond assessing patterns of individual diet variation, a key question is to identify the factors determining this variation. Individual variation, mainly in terms of diet but also along other niche dimensions, is common and can be generated by many processes, including intra-specific competition but also sexual dimorphism, ontogenetic niche shift, physiological requirement, and/or behaviour (see Araùjo *et al.* 2011 and Bolnick *et al.* 2003). Individual diet variation in particular was addressed by the Optimal Foraging Theory (OFT), which suggests that, although an individual is phenotypically able to consume a wide diversity of prey items, it may adopt different diets depending on their benefits in terms of energetic value per handling time, which may in turn depend on the individual's phenotype and state (Schoener 1971; Werner & Hall 1974; Svanbäck & Bolnick 2005). Consequently, phenotypic or state variation between conspecifics may underlie individual diet variation (Araùjo *et al.* 2011). It is thus surprising that phenotypic variation between conspecifics was never directly investigated as a potential cause of individual diet variation in a test of the NVH.

Another unexplored aspect of the NVH is its potential link with the ecological functions performed by species. It is generally admitted that the variation of species and individual traits or niches influences ecosystem functioning (Petchey & Gaston 2006; Cianciaruso *et al.* 2009). Furthermore, species performing peculiar ecological functions necessitating highly specialized traits, are expected to have a narrow ecological niche and to exhibit weak individual variation. In contrast, species performing a variety of functions are supposed to have a broad niche and display large individual variation. It may thus be hypothesised that species belonging to the same functional group should be located at the same position along the gradient niche breadth/individual variation expected from the NVH within a community. In other words, beyond investigating whether the NVH holds between species within a community, one may wonder whether it holds between functional groups within a community. An interesting point here is that, in general, studies of functional ecology focus on the trophic component of the ecological niche, since trophic relationships are related to one of the main ecosystem functions, i.e. energy and mass transfer; in parallel, a classical approach to assess niche variation and estimate competition is to focus on food resources use, i.e. the trophic niche. It is thus surprising that, to our best knowledge, these two approaches have not been merged.

The aim of this paper was to test whether the Niche Variation Hypothesis holds between species within a community and to relate it to competition, species functional identity (membership to a functional group), and patterns of individual variation and their determinants. An assemblage of 16 marine fish species, chosen to represent a diversity of foraging strategies and feeding habits, belonging to the ichthyological community of the eastern English Channel were taken as a case study. Fish is a taxa well known for exhibiting the ability to feed on a wide diversity of prey items (Bolnick *et al.* 2003; Bellwood *et al.* 2006) and a high level of diet variation between conspecifics (Svanbäck & Persson 2004; Svanbäck & Bolnick 2007; Araùjo *et al.* 2008; Post *et al.* 2008). Characteristics of species trophic niches, namely species trophic niche breadth, species diet similarity (niche overlap as an indicator of potential inter-specific competition), and individual diet variation were estimated. Firstly, correlations expected from the NVH, i.e. a positive correlation between species trophic niche breadth and individual diet variation, a negative correlation between species trophic niche breadth and species diet similarity, a proxy for inter-specific competitive pressure, and a negative correlation between individual variation and species diet similarity, were tested. In a second step, species' membership to a functional group was estimated based on their functional traits (related to their usual habitat, foraging strategy and swimming mode) and correlations expected from the NVH were tested between and within functional groups. Finally, patterns of individual niche occupation were identified and when individual variation was detected, its potential causes among habitat variation and phenotypic variation were investigated.

IV.3 Materials and methods

IV.3.1 Sample collection

Sixteen species of fish (horse mackerel, *Trachurus trachurus*; herring, *Clupea harrengus*; pilchard, *Sardina pilchardus*; mackerel, *Scomber scombrus*; sprat, *Sprattus sprattus*; plaice, *Pleuronectes platessa*; sole, *Solea solea*; cod, *Gadus morhua*; whiting, *Merlangius merlangus*; skate, *Raja clavata*; smoothhound, *Mustelus asterias*; catshark, *Scyliorhinus canicula*; surmullet, *Mullus surmuletus*; seabass, *Dicentrarchus labrax*; red gurnard, *Chelidonichthys cuculus*; tub gurnard, *Chelidonichthys lucerna*) were collected in the eastern English Channel during the Channel Ground Fish Survey (CGFS), operated by IFREMER in October 2009 (**Fig. IV.1**). Fish were caught on board RV “Gwen Drez” by towing a high opening demersal trawl (GOV) with a cod-end of 20 mm stretched mesh for 30 minutes at a speed of approximately 3.5 knots. A stratified sampling scheme was used, the area being subdivided into 15’ x 15’ rectangles in which the GOV trawl was fished at least once. For each fish species, all present sizes were sampled. Following their capture, species were identified and individuals were labelled, frozen on board with liquid nitrogen to instantly stop digestion, and kept frozen until further use. In the laboratory, the fish were defrosted, dissected to extract their digestive tract and the contents removed and kept in Petri dishes for analysis.

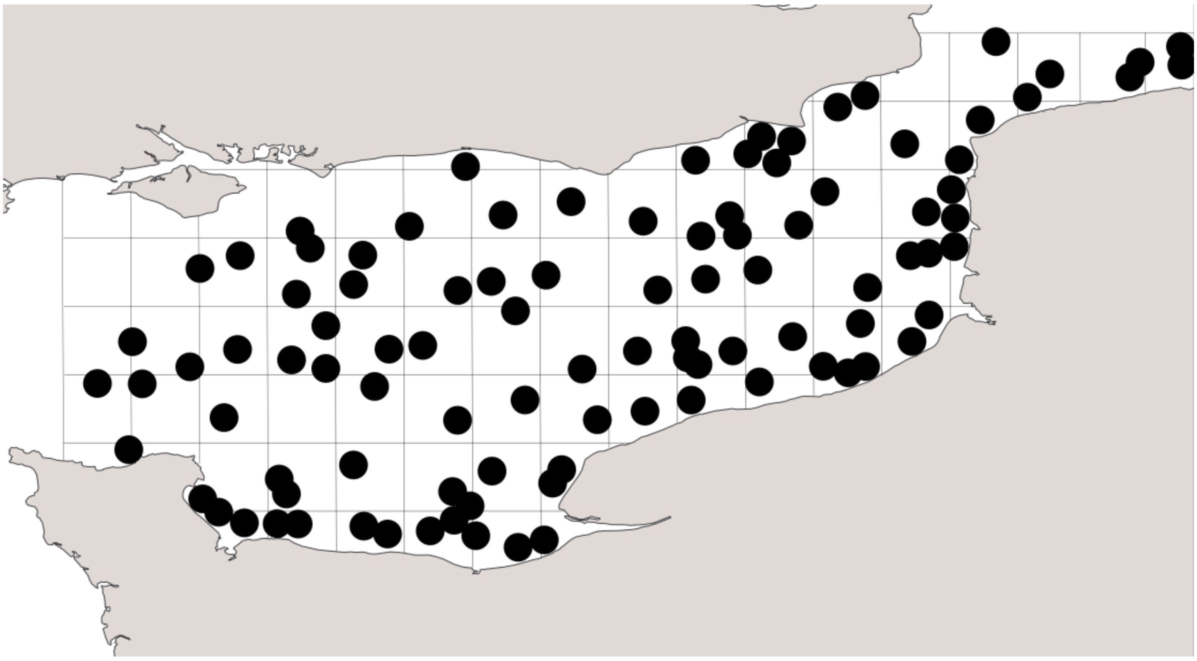


Figure IV.1: Map of the sampling area and related stratified scheme.

IV.3.2 Digestive tract analysis

Prey were identified to the lowest possible taxon under a stereomicroscope Olympus SZX 16®, sorted, counted and weighted (0.1g) in 853 available and non-empty digestive tracts. 96 empty stomachs were excluded from analysis and parasites (plathelminths and nematodes) were not taken into account in fish diet. Prey items were then grouped into 41 categories combining taxonomic level and functional characteristics (see **PhD ANNEXE 3** for a complete description of prey categories). Then, for each individual k of species j, the proportion p_{ijk} of each prey category i in the individual's diet was calculated on the basis of the Geometric Mean (GM) of prey number and weight such as:

$$p_{ijk} = \frac{\sqrt{W_{ijk} \times N_{ijk}}}{\sum_{i'} (\sqrt{(W_{i'jk} \times N_{i'jk})})} = \frac{g_{ijk}}{\sum_{i'} g_{i'jk}} \qquad (1)$$

where W_{ijk} and N_{ijk} are the total weight and the total number of prey of category i in the digestive tract content of individual k from fish species j. We used GM to calculate prey category proportion in individuals' diet as a new index to compensate for prey importance in weight and number. Combining these two aspects is considered effective in depicting dietary importance of prey categories, since it allows to take into account energy consumption (prey biomass, W_{ijk}) and foraging behaviour (prey count, N_{ijk}) (see Hyslop 1980 for discussion). The same index was computed at the species level, p_{ij}, to calculate the proportion of prey category i in the diet of fish species j taken as a whole by simply replacing W_{ijk} and N_{ijk} by $W_{ij} = \sum_k W_{ijk}$ and $N_{ij} = \sum_k N_{ijk}$ in equation (1).

IV.3.3 Statistical analyses

Testing predictions from the Niche Variation Hypothesis

First, trophic niche breadth was determined for each species j using Levin's index B_j based on species diet p_{ij}:

$$B_j = \frac{1}{\sum_i p_{ij}^2} \qquad (2)$$

This index tends to 0 when the species has a narrow trophic niche (feeds only on one prey category), and increases with niche breadth (increasing diversity of food resources, Levin 1968).

Second, diet similarity between species (niche overlap) was used as an indicator of potential inter-specific competition. It was calculated using pairwise proportional similarity indices $PS_{jj'}$ between species j and j' (Schoener 1968):

$$PS_{jj'} = 1 - 0.5\sum_{i} \left| p_{ij} - p_{ij'} \right| \quad (3)$$

$PS_{jj'}$ equals 1 when species j and j' have perfectly similar diets (proportions p_{ij} are $p_{ij'}$ equal), and 0 when species j and j' have completely dissimilar diets (see **ESM IV.1** for pairwise values of $PS_{jj'}$). For each species, the mean pairwise similarity index, $\overline{PS_{jj'}} = \sum_{j'} PS_{jj'} / (n-1)$, *n* being the number of species under study, was used as an estimate of overall potential inter-specific competitive pressure.

Third, for each species, among-individual diet variation was estimated by the index E_j proposed by Araùjo *et al.* (2008). E_j is based on the calculation of the density of connections between individuals across the network, and ranges from 0 when all individuals are connected because there is no diet variation among them, i.e. all individuals have the same diet, and increases up to 1 with individual diet variation.

Finally, the correlations between the indices described above (B_j, $\overline{PS_{jj'}}$ and E_j) predicted by the Niche Variation Hypothesis were tested using Pearson correlations across all species. *P*-values of significance tests were corrected to account for multiple comparisons using the Holm method. See **Fig. IV.2** for analytical procedure.

Investigating functional bases of the Niche Variation Hypothesis

Each species was characterized by nine functional traits related to usual habitat (place in the water column, usual depth, and habitat), foraging strategy (foraging type, behaviour of young and adult, foraging time, and trophic level) and swimming mode (see **ESM IV.2** for species functional traits). Functional groups of species were identified in the functional tree obtained by hierarchical clustering on the functional trait matrix using the Gower's distance and the average method as advised by Legendre & Legendre (1998) and Petchey & Gaston (2002). In order to estimate if functional identity is implicated in the correlations predicted by the NVH, the total correlations across species between B_j, $\overline{PS_{jj'}}$ and E_j (see above) were decomposed in between-group correlations and within-group correlations (Pedhazur 1997). This decomposition was meant to evaluate whether the NVH predictions were supported across functional groups and across species within functional groups, respectively. See **Fig. IV.2** for analytical procedure.

Assessing patterns and causes of individual occupation of species trophic niche

The patterns of individual diet variation, in other words the patterns of species trophic niche occupation by conspecifics, were investigated using the index of clustering $C_{ws,j}$ proposed by Araùjo *et al.* (2008). $C_{ws,j}$ compares the average density of connections, represented here by pairwise proportional similarity indices $PS_{kk'}$ between pairs of individuals (k,k'), across the network of diet overlap in the whole population with the average density of connection around individuals. $C_{ws,j}$ is equal to 0 when individuals use resources randomly, whereas $C_{ws,j}$ tends to -1 if individuals specialize on a subset of resources so that their diets are over-dispersed. In contrast, $C_{ws,j}$ will be positive and tend to +1 when the population is composed of one or more clusters of individuals sharing common resources.

Following Araùjo *et al.* (2008), when a clustered pattern was detected, individuals' memberships to clusters were assessed based on the strength of dietary similarity between individuals. More precisely, the diet overlap $PS_{kk'}$ between individuals k and k' was considered as strong when it was larger than its population average $\overline{PS_{kk'}}$. A similarity binary matrix between conspecifics was then created by attributing to each pair of individuals (k,k') a value of 1 when $PS_{kk'} > \overline{PS_{kk'}}$ and 0 otherwise. Individual membership to clusters was then determined by hierarchical clustering on this similarity binary matrix, using Euclidean distance modified for binary data and the Ward method. The computation of the ratio within- and between-clusters average distances (wb_j) on the resulting clustering was finally used to distinguish the random pattern ($wb_j > 0.5$ combined with a $C_{ws,j}$ close to 0) and the pattern that included a group of few outliers ($wb_j < 0.5$ combined with a $C_{ws,j}$ close to 0).

In order to investigate potential sources of individual variation and clustering, difference between clusters in terms of individuals' sex, maturity stage, body size, and depth at collection site were tested by one-way ANOVAs with cluster's membership as explanatory variable. Assumptions of linear modelling were verified and data transformed whenever necessary. These were intended to test for clustering due to dietary polymorphism linked to sexual dimorphism (sex), physiological requirement (maturity stage), ontogenetic shift (body size) and habitat variation (depth). In case of patterns with one cluster and a few outliers, randomization tests were used to test for differences between the cluster and outliers instead of ANOVAs because of the strong inequality in sample size between the cluster and the outliers (Manly 2007). See **Fig. IV.2** for analytical procedure.

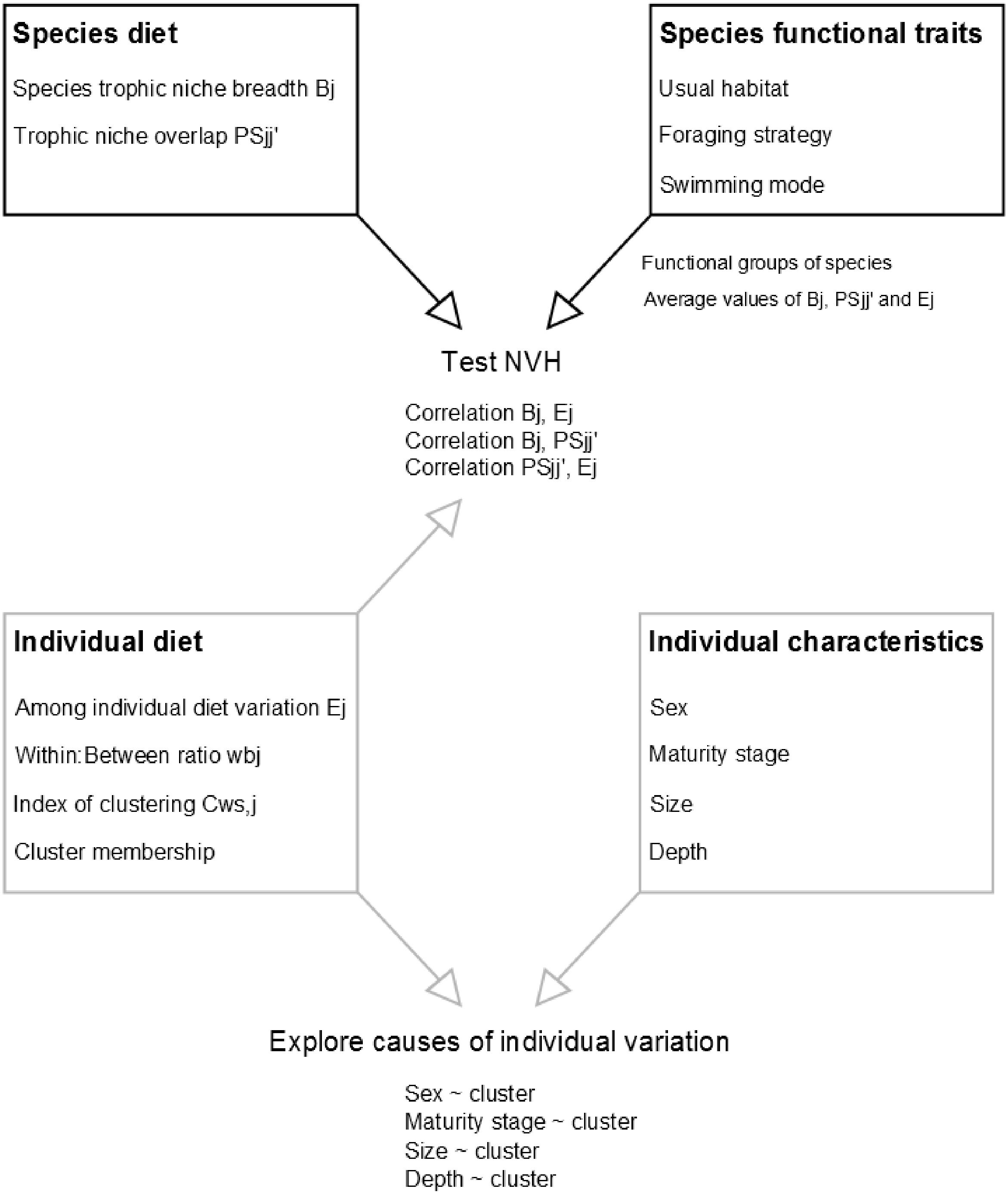


Figure IV.2: Scheme of analytical strategy.

Levin's indices were computed with the package "vegan" (Oksanen *et al.* 2012) of the software R (R Core Team 2012), E_j, $C_{ws,j}$, and $PS_{jj'}$ were computed using the package "RinSp" (Zaccarelli *et al.* 2013), and wb_j were computed with package "fpc" (Hennig 2013)

IV.4 Results

IV.4.1 Predictions from the Niche Variation Hypothesis

Species under study exhibited a wide range of values for species niche breadth ($1.18 < B_j < 10.20$), and the other trophic indices ranged from 0.09 to 0.31 for average niche overlap $PS_{jj'}$, from 0.30 to 0.90 for the index of among-individual diet variation E_j, and finally from – 0.13 to 0.21 for the index of clustering $C_{ws,j}$ (**Table IV.1**, see also **ESM IV.1** for pairwise values of $PS_{jj'}$). Species trophic niche breadth B_j significantly increased with the index of among-individual diet variation E_j ($R^2 = 0.59$, **Fig. IV.3 a**, solid circles), and also with species diet similarity $PS_{jj'}$ ($R^2 = 0.66$, **Fig. IV.3 b**, solid circles). In contrast, the correlation between diet similarity $PS_{jj'}$ and among-individual diet variation E_j was not significant (**Fig. IV.3 c**, solid circles).

Table IV.1: Species trophic niche characteristics, namely species trophic niche breadth (B_j), average trophic niche similarity ($\overline{PS_{jj'}}$), among-individual diet variation (E_j), index of clustering ($C_{ws,j}$), and within-between ratio (wb_j) used to discriminate cluster-outlier patterns of individual variation from others.

Species	B_j	$\overline{PS_{jj'}}$	E_j	$C_{ws,j}$	wb_j
Horse mackerel	4.51	0.28	0.73	-0.03	0.54
Herring	2.62	0.25	0.30	0.01	0.30
Pilchard	1.18	0.17	0.52	0.08	0.34
Mackerel	4.62	0.21	0.82	0.41	0.46
Sprat	1.59	0.18	0.47	0.05	0.41
Plaice	2.38	0.09	0.86	0.13	0.60
Sole	5.60	0.18	0.82	-0.04	0.59
Cod	10.20	0.26	0.87	0.07	0.76
Whiting	4.92	0.25	0.82	0.21	0.63
Skate	7.35	0.30	0.78	-0.13	0.65
Smoothhound	6.88	0.29	0.67	-0.04	0.76
Catshark	7.26	0.31	0.66	-0.04	0.76
Surmullet	5.29	0.23	0.76	-0.04	0.62
Seabass	7.19	0.27	0.90	0.23	0.63
Red gurnard	5.78	0.30	0.77	0.03	0.75
Tub gurnard	6.53	0.27	0.83	0.09	0.64

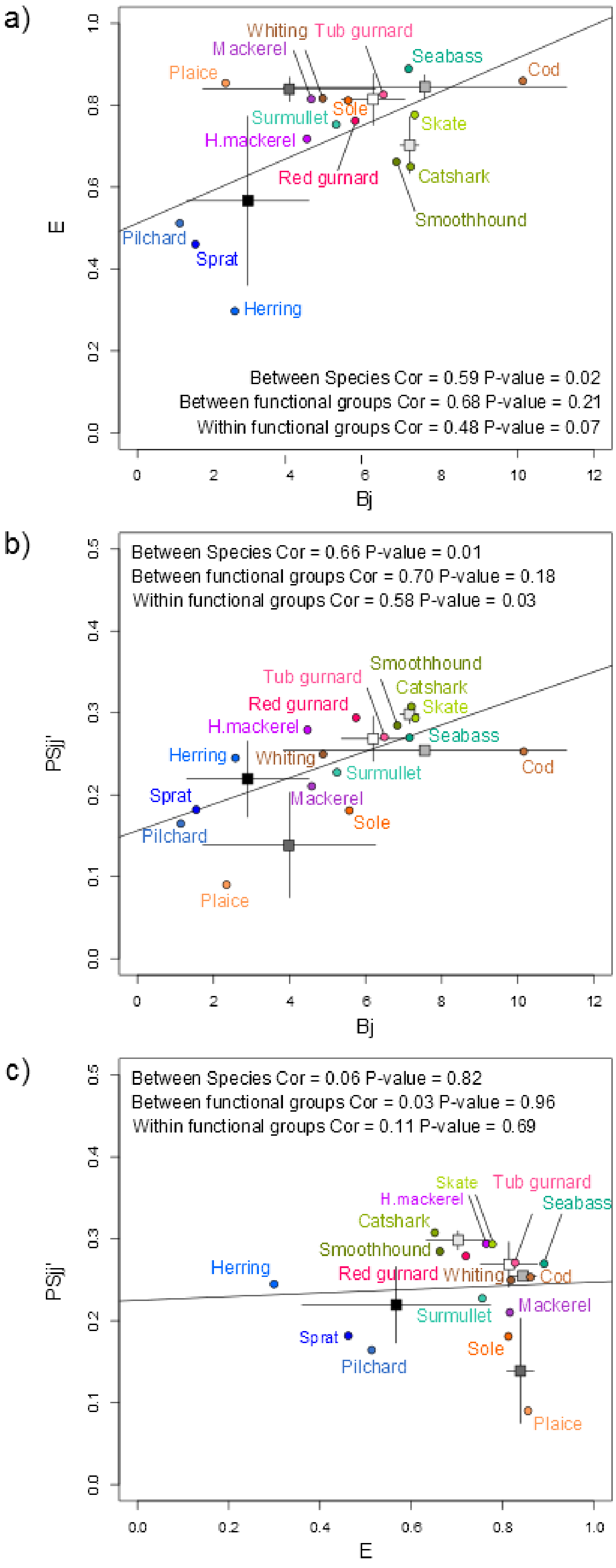


Figure IV.3: Correlations between trophic indices predicted by the Niche Variation Hypothesis. a) correlation between species trophic niche breadth B_j and individual variation E_j. b) correlation between B_j and species trophic niche similarity $\overline{PS_{jj'}}$. c) correlation between E_j and $\overline{PS_{jj'}}$. Index values for species are depicted by solid circles. Indices for functional groups (calculated as average index values across species affiliated to this group) and their standard deviations are depicted by solid squares and vertical-horizontal bars, respectively. *P*-value < 0.05 *.

IV.4.2 Functional view of the Niche Variation Hypothesis

The functional tree depicted five functional groups of fish species (**Fig. IV.4**, see **ESM IV.2** for species functional traits). The first one included schooling pelagic feeders, namely horse mackerel, herring, pilchard, mackerel and sprat. The second group was composed of flat benthic feeders, namely plaice and sole. The third group comprised diurnal omnivorous, i.e. cod and whiting. The fourth functional group contained nocturnal demersal feeders: skate, smoothhound and catshark. The last functional group comprised solitary demersal feeders, i.e. surmullet, seabass, red and tub gurnards. The correlations between B_j, $\overline{PS_{jj'}}$ and E_j predicted by the NVH were not significant when considered across functional groups (**Fig. IV.3 a, b and c**, solid squares). However, the values of these between-group correlations were very similar to those of the total correlations across all species, the difference in significance levels being related to the decrease in the number of points from 16 to 5. Interestingly, the within-group correlations, i.e., the correlations across species but within functional groups, were also close to the total correlations and there significance levels were very similar.

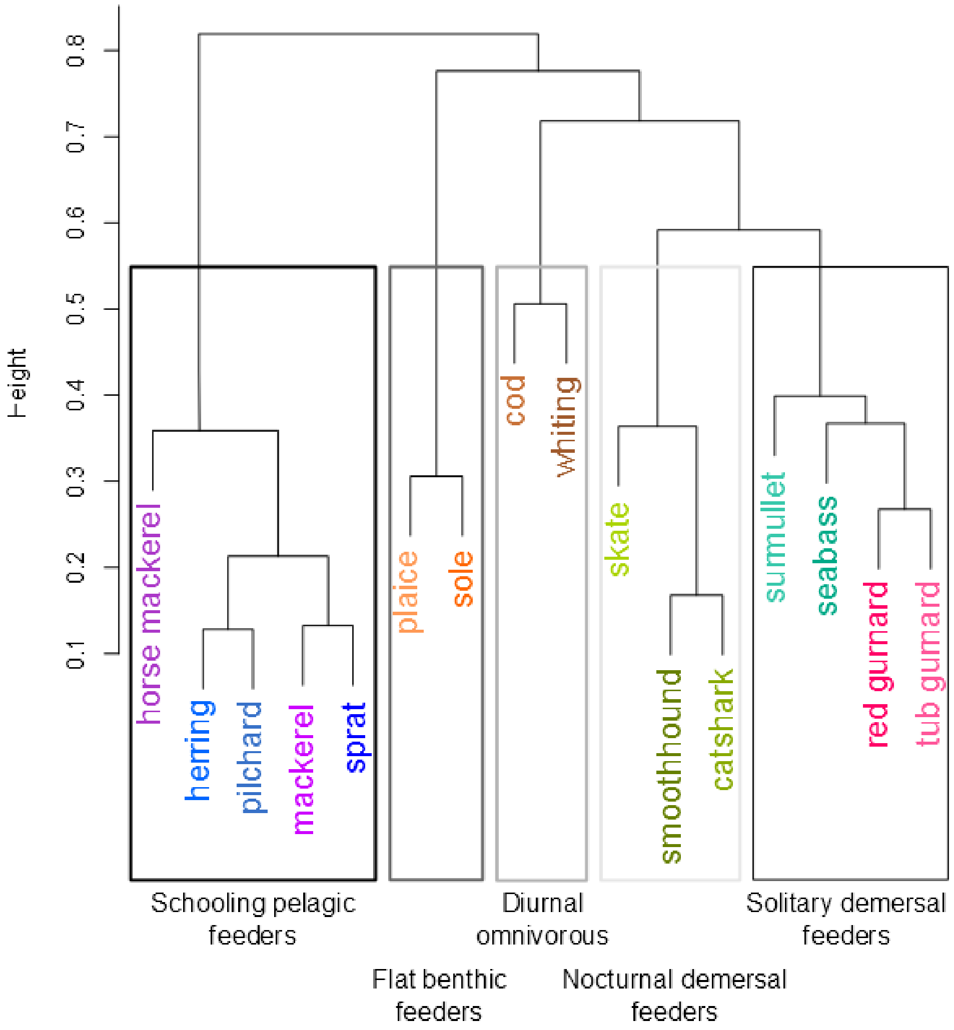


Figure IV.4: Hierarchical clustering on species functional traits (see **ESM IV.2** for description), depicting five functional groups of fish species.

IV.4.3 Patterns and causes of individual occupation of species trophic niche

Four different patterns of individual occupation of species trophic niche were detected, i.e. random, overdispersed, cluster-outliers and clustered. Eight species, namely catshark, red gurnard, sole, tub gurnard, smoothhound, surmullet, cod and horse mackerel, exhibited a random distribution of individuals within their trophic niche ($C_{ws,j} \approx 0$ and $wb_j > 0.5$, **Fig. IV.5 a to h**). Individuals were overdispersed, $C_{ws,j} < 0$, for a single species, i.e. skate (**Fig. IV.5 i**).

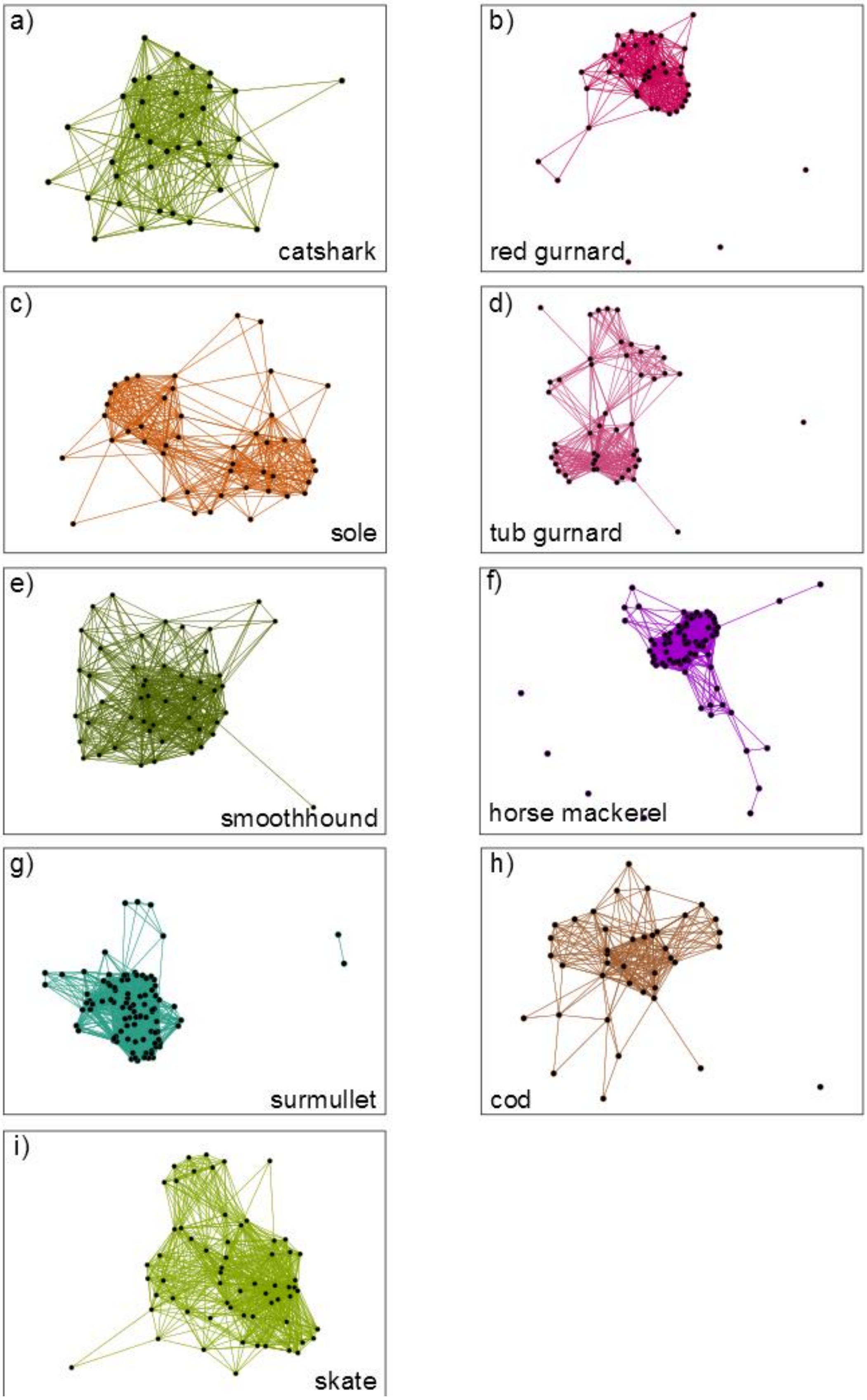


Figure IV.5: Network representation of individual occupation of species trophic niche for species that exhibited a random (a to h) or overdispersed distribution (i).

Three species, herring, sprat, and pilchard, displayed a cluster-outliers pattern of individual niche occupation ($C_{ws,j} \approx 0$ and $wb_j < 0.5$), i.e. comprising a single cluster of individuals and a few outliers (**Fig. IV.6 a, c, and e**). For herring and sprat, a significant difference in size between clustered individuals and outliers was detected by randomization tests, while pilchard exhibited a significant difference in sexual composition between clustered individuals and outliers (**Fig. IV.6 b and d**).

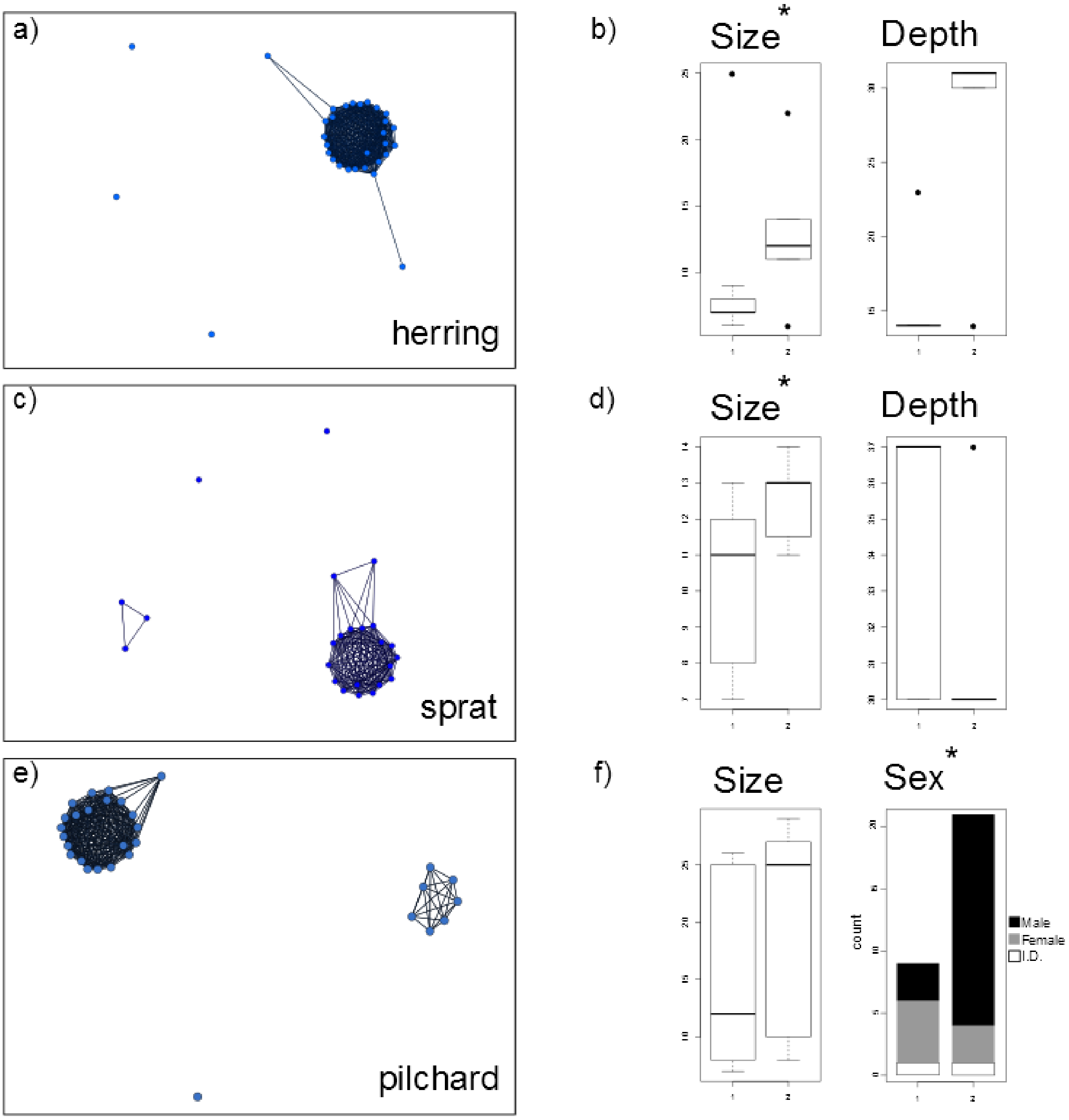


Figure IV.6: Network representation of individual diet variation for species that exhibited a pattern characterised by a single cluster of individuals and a few outliers. Boxplots represent individual characteristics that significantly differed between clustered (1 on x-axis) ant outlier individuals (2 on x-axis) for at least one species. *: p<0.05, **: p<0.01; ***:p<0.001.

The pattern of individual occupation of the trophic niche of the four last species, namely mackerel, whiting, plaice and seabass, was characterised by several clusters of individuals (**Fig. IV.7 a, c, e, g**), as indicated by positive $C_{ws,j}$ values ranging from 0.13 to 041 (**Table IV.1**). For mackerel, significant differences in terms of size and depth were detected by ANOVAs between the four clusters of individuals (**Fig. IV.7 b**) whereas for plaice, a significant difference in sexual composition was detected between the four clusters (**Fig. IV.7 b**). No difference was observed for whiting and seabass whatever the individual characteristic considered (**Fig. IV.7 d, f and h**).

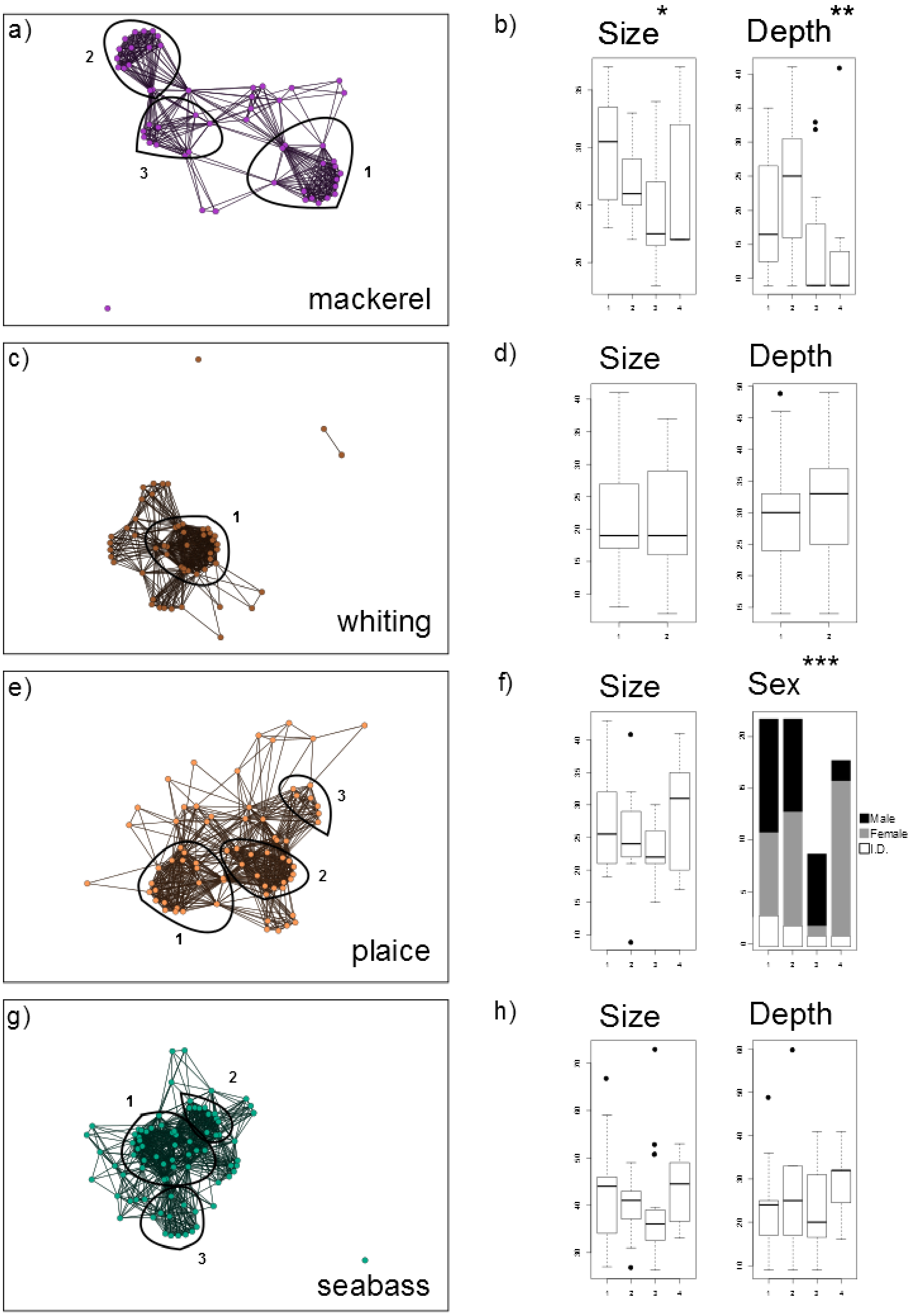


Figure IV.7: Network representation of individual diet variability for species that exhibited a pattern characterised by several clusters of individuals. In a), e), g) the first three clusters are surrounded, the fourth one being remaining individuals. In c), the first cluster is surrounded, the second one being remaining individuals. Boxplots represent individual characteristics that significantly differed between clusters for at least one species. *: $p<0.05$, **: $p<0.01$; ***:$p<0.001$.

IV.5 Discussion and perspectives

This study successfully supported the Niche Variation Hypothesis between species within a community. A positive correlation was observed between species trophic niche breadth and individual diet variation. However, other predictions derived from the competitive basis of the Niche Variation Hypothesis were not confirmed. Species diet similarity, used as a proxy for potential inter-specific competition, increased with species niche breadth and was unrelated to with individual variation whereas a negative relationship was expected with both. Investigation of the causes of niche variation highlighted that species niche characteristics were partly related to their functional identity, correlations across functional groups being very close to total correlations, but not only as correlations across species within functional groups were also alike. In other words, the NVH seems to hold at various levels of organization: across species within the community, across functional groups within the community, and across species within functional groups. Individual characteristics were also partly involved in niche variation as individuals occupied species trophic niche according to different patterns that were influenced by individual body size, sex and/or habitat (depth) for some species.

IV.5.1 NVH and competition

The expansion of a species niche breadth, known as “ecological release”, is intuitively expected to originate in (i) the simultaneous expansion of all individual niches (here individuals’ diets), referred to as the hypothesis of “parallel release”, and/or (ii) the increase in variation between individual niches, i.e. the Niche Variation Hypothesis (Bolnick *et al.* 2010). Our study clearly demonstrated that, within the same community, species trophic niche expansion is positively related to increasing individual diet variation, according to the Niche Variation Hypothesis. To our best knowledge, it is the first time that the NVH is documented within the same community and across trophic levels (Svanbäck & Bolnick 2007; Woo *et al.* 2008; Tinker *et al.* 2012).

Species trophic niche breadth is expected to result from the balance between inter-specific competition that constrains species niche and individual variation, and intra-specific competition that causes individual niche diversification and species niche expansion (Van Valen 1965; Svanbäck & Bolnick 2005, 2007). An interesting feature was the contradiction between this prediction and the positive relationships between species trophic niche breadth

B_j and between-species diet similarity $\overline{PS_{jj'}}$, used as a proxy for niche overlap and thus inter-specific competition. In the same line, individual variation is expected to result from the balance between the constraining effect of inter-specific competition, and the diversifying effect of intra-specific competition (Van Valen 1965; Svanbäck & Bolnick 2005, 2007), but no correlation between species niche overlap and individual diet variation was detected in our study.

These two unexpected results may have several explanations. First, the abundance of resources may be sufficient to sustain the fish community without implying competitive interactions between species and/or individuals when their diet overlap. Second, the sub-sample of species used in this study may provide a misrepresentation of the actual community, so that actual inter-specific competitive pressures for food resources in the community have been wrongly estimated by our measures of diet similarity. It is however important to remind that the current organization of trophic niches results from evolutionary history driven by past competitive pressures. It is therefore possible that there is currently weak inter-specific competition because past competition implied that species have evolved to forage on most abundant prey items in order to relax competition and allow their coexistence. It would be interesting, for future research, to test the relationship between current inter-specific competition and species niche breadth within communities in a limited resources context, using for example mesocosm experiments.

IV.5.2 A functional point of view

Using species from the same community allowed us to go further than testing the total correlations across species resulting from the NVH and to attempt to identify other factors than the competitive balance that may be implicated in the NVH, notably functional identity. Membership to a functional group was expected to be related to trophic niche characteristics, since some functions performed by species may necessitate ecological specialization and thus a narrow ecological niche. In agreement with this expectation, the correlation between trophic niche breadth and individual variation across functional groups was similar to that across species, though not significant because of a low statistical power due to the fact that the assemblage contained only 5 functional groups. This implies that the way ecological space is occupied by species and the organization of species niches within a community is related to species function. Most importantly, it suggests that, besides competition, the function performed by a species may also constrain its niche breadth and individual variation. To our knowledge, this aspect of the NVH was never investigated before and was brought by the community approach used in this study. However, the fact that the correlation between trophic niche breadth and individual variation across species but within functional groups was also similar to the total correlation suggests that functional identity is not the only source of niche variation and that several levels of biological organization are supporting it. Our approach is however limited by the small number of functional groups in the studied fish assemblage. It would thus be important to further investigate the respective contributions of between- and within-functional groups variation to the NVH within communities by considering richer communities in terms of functional groups in order to determine the exact relationship between functional identity and niche characteristics.

IV.5.3 Patterns of individual variation

The root of the NVH remains the niche variation among conspecifics. This study allowed to describe several patterns of individual variation corresponding to different individual occupation of species trophic niches: overdispersion, random distribution, clustered distribution and distribution combining clusters and outliers. As expected, generalist species, i.e. those with broad trophic niche, exhibited several patterns of individual variation composed of (i) specialist individuals (overdispersion, e.g. skate), (ii) a combination of generalist and specialist individuals (random distribution, e.g. cod), and (iv) several specialized clusters (e.g. mackerel, Araùjo *et al.* 2011, Bolnick *et al.* 2003, Svanbäck & Bolnick 2005). Such results greatly support the NVH instead of the “parallel release” hypothesis, since none of our species with a large trophic niche was composed of a single cluster of generalist individuals, i.e. with large individual trophic niches. They highlight that trophic generalist marine fish populations are generally based on individual diversification of trophic niche. Such difference between conspecifics may have important implications on population and community dynamics, since individual specialization is known to affect population stability, food web structure, or inter-specific interactions (Bolnick *et al.* 2003; Svanbäck & Persson 2004; Araùjo *et al.* 2011). Individual specialization may also have crucial evolutive consequences as individuals with different trophic niches may differ in fitness, intra-specific diet variation being then a target for natural selection. The cluster-outliers pattern, exhibited by specialist species, i.e. those with narrow species trophic niche and for which individual diet variation was the smallest, was particularly interesting in this respect and raised the question about fitness advantage or disadvantage of outlier individuals compared to clustered individuals. Further investigations, such as mesocosm experiments, are needed to better understand the evolutionary consequences of individual variation, particularly for specialist species (Bolnick *et al.* 2003). However, not all sources of intra-specific variation are evolutionary relevant, which highlight the need to investigate these sources for individual diet variation.

IV.5.4 Causes of individual variation

Individual diet variation, and thus individual trophic niche variation, were often described in animals and sometimes related to intra-specific competition (Araùjo *et al.* 2008). It is not possible to exclude this hypothesis here as no direct measure of intra-specific competition was available, but our results on inter-specific competition suggest that food resources are not limiting in the fish community (see subsection "NVH and competition"). Consequently, current intra-specific competition for food is unlikely to explain individual trophic niche variation. Diet variation among conspecifics was also described as resulting from differences in foraging area between individuals (Estes *et al.* 2003). Habitat variation is indeed associated with variation in prey availability and diversity. It may therefore promote diet diversification across individuals foraging in different habitats and thus on different prey. Depth at catch, used as a proxy for habitat, was related to individual diet variation for mackerel only, suggesting habitat variation as a source of individual diet variation for this species but not for the others. Depth may not be a relevant proxy for habitat, which would explain the seemingly weak contribution of habitat variation to individual diet variation across the studied species. However, marine habitats and communities are generally strongly structured by depth, especially in continental shelf areas as the eastern English Channel (Foveau *et al.* 2013). A more likely hypothesis would be that, for most fish species, variation in available prey items is not a factor promoting individual diet variation, and thus that individual niche diversification does not depend on habitat heterogeneity within its distribution area, at least at meso-scale such as in our study.

Diet variation among conspecifics is more generally attributed to phenotypic variation, in accordance with Optimal Foraging Theory (Bolnick *et al.* 2003; Svanbäck & Bolnick 2008), which states that an individual will choose to consume a prey item so as to maximize its fitness benefits. Consequently, the diet of an individual is expected to depend on prey traits (ability to avoid predator, chemical or morphological defense etc.) but also on its own phenotype (polymorphism in size, morphology, physiological requirements, experience, behaviour, or social status). In our study, size had a minor effect on diet variation between conspecifics as it was associated with individual occupation of species trophic niche for 3 species only (herring, sprat and mackerel). However, it is worth noticing that all individuals in this study were at the juvenile or adult stage, and thus that the major ontogenic transition in fish life-cycle, namely metamorphosis from the larval to the juvenile stage, was omitted. Fish are well known to exhibit ontogenetic niche shifts and it is likely that, considering larger size ranges related to more life-stages, ontogeny would emerge as a factor explaining individual niche variation (Polis 1984). Physiological requirements are also supposed to explain individual trophic niche variation (Svanbäck & Bolnick 2008). Besides the fact that they may be related to individuals' life-stage and thus size, they can also depend on maturity stage and sex (ecological sex dimorphism). Sex had a significant but minor effect on individual diet variation for two species only, namely pilchard and plaice. It may thus be hypothesized that these two species exhibited a certain degree of dietary sexual dimorphism, but more studies are needed to assess if it concerns other fish species. Maturity stage, on the contrary, appeared to have implication for individual niche variation.

In the original approach of the Niche Variation Hypothesis (Van Valen 1965), individual variation in trophic morphology was related to species ecological niche breadth. It is indeed expected that mouth gape in fish or beak width in birds, for example, will determine prey items a predator can consume, and thus that variability in diet-related morphological traits between conspecifics may imply diet variability within the population. A complementary approach to this study would thus be to test whether morphological and behavioural polymorphism are implicated in the relationship between individual niche variation and species niche breadth across species within a community and thus potentially at the origin of the Niche Variation Hypothesis within communities (Bolnick *et al.* 2010).

Acknowledgments

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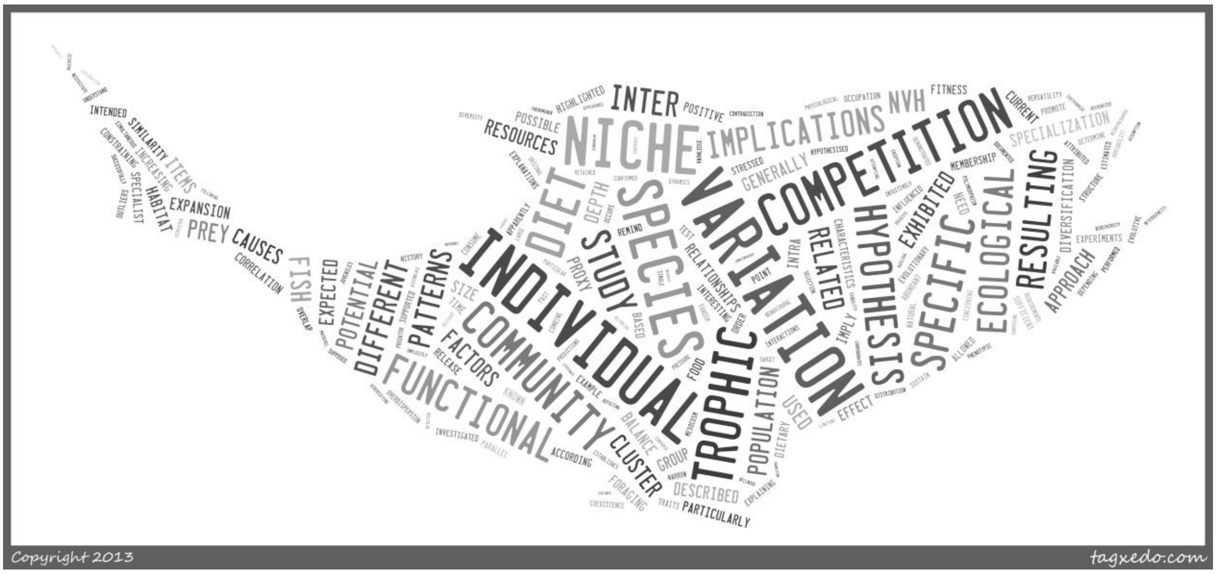
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IV.6 References

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IV.7 Supplementary materials

ESM IV.1. Pairwise trophic niche similarity estimated with Proportional Similarity indices ($PS_{jj'}$) between each pair of species and considered as an estimation of inter-specific trophic competition.

species	Red gurnard	Herring	Seabass	Cod	Whiting	Surmullet	Smoothhound	Plaice	Skate	Pilchard	Mackerel	Catshark	Sole	Sprat	Horse mackerel	Tub gurnard
Red gurnard		0.16	0.31	0.29	0.41	0.27	0.51	0.03	0.49	0.06	0.30	0.45	0.16	0.06	0.39	0.55
Herring	0.16		0.12	0.07	0.17	0.15	0.12	0.04	0.16	0.72	0.20	0.20	0.06	0.86	0.55	0.14
Seabass	0.31	0.12		0.59	0.34	0.19	0.41	0.11	0.37	0.06	0.22	0.29	0.22	0.06	0.20	0.61
Cod	0.29	0.07	0.59		0.27	0.20	0.50	0.18	0.40	0.05	0.20	0.30	0.21	0.06	0.17	0.36
Whiting	0.41	0.17	0.34	0.27		0.26	0.20	0.07	0.37	0.07	0.43	0.29	0.21	0.07	0.26	0.40
Surmullet	0.27	0.15	0.19	0.20	0.26		0.28	0.21	0.27	0.05	0.13	0.48	0.55	0.03	0.17	0.23
Smoothhound	0.51	0.12	0.41	0.50	0.20	0.28		0.07	0.62	0.05	0.23	0.51	0.18	0.03	0.31	0.30
Plaice	0.03	0.04	0.11	0.18	0.07	0.21	0.07		0.07	0.01	0.03	0.20	0.31	0.00	0.02	0.05
Skate	0.49	0.16	0.37	0.40	0.37	0.27	0.62	0.07		0.06	0.27	0.45	0.17	0.06	0.29	0.40
Pilchard	0.06	0.72	0.06	0.05	0.07	0.05	0.05	0.01	0.06		0.09	0.06	0.03	0.85	0.31	0.06
Mackerel	0.30	0.20	0.22	0.20	0.43	0.13	0.23	0.03	0.27	0.09		0.33	0.04	0.10	0.38	0.26
Catshark	0.45	0.20	0.29	0.30	0.29	0.48	0.51	0.20	0.45	0.06	0.33		0.40	0.06	0.39	0.25
Sole	0.16	0.06	0.22	0.21	0.21	0.55	0.18	0.31	0.17	0.03	0.04	0.40		0.02	0.08	0.14
Sprat	0.06	0.86	0.06	0.06	0.07	0.03	0.03	0.00	0.06	0.85	0.10	0.06	0.02		0.45	0.06
Horse mackerel	0.39	0.55	0.20	0.17	0.26	0.17	0.31	0.02	0.29	0.31	0.38	0.39	0.08	0.45		0.28
Tub gurnard	0.55	0.14	0.61	0.36	0.40	0.23	0.30	0.05	0.40	0.06	0.26	0.25	0.14	0.06	0.28	

ESM IV.2: Species functional traits.

Species	**Water**	**Swim**	**Forage**	**Depth**	**Habitat**	**Young**	**Adult**	**Time**	**TL**
Horse mackerel	semi-pelagic	carangiform	school	0-200	shelf	school	school	everytime	3.64
Herring	pelagic	carangiform	school	0-200	all	school	school	diurnal	3.23
Pilchard	pelagic	carangiform	school	25-100	coastal	school	school	NA	3.05
Mackerel	pelagic	carangiform	school	0-200	shelf	school	school	diurnal	3.65
Sprat	pelagic	carangiform	school	10-150	NA	school	school	diurnal	3.00
Plaice	benthic	side	burry	10-50	shelf	NA	NA	nocturnal	3.30
Sole	benthic	side	burry	10-60	shelf	alone	alone	NA	3.10
Skate	benthic	rajiform	NA	10-300	shelf	alone	NA	nocturnal	3.80
Smoothhound	demersal	anguiliform	NA	0-100	shelf	NA	NA	NA	3.71
Catshark	demersal	anguiliform	school	10-110	shelf	school	alone	nocturnal	3.70
Cod	bentho-pelagic	carangiform	NA	0-600	shelf	both	NA	nocturnal	4.42
Whiting	bentho-pelagic	subcarangiform	NA	10-200	all	NA	NA	NA	4.37
Surmullet	demersal	subcarangiform	searcher	5-60	NA	NA	NA	NA	3.42
Seabass	demersal	subcarangiform	NA	10-100	coastal	alone	school	diurnal	3.79
Red gurnard	demersal	subcarangiform	searcher	30-250	shelf	NA	NA	diurnal	3.85
Tub gurnard	demersal	subcarangiform	searcher	20-318	shelf	NA	NA	diurnal	3.65

Chapter V Functional diversity is predicted by morphological diversity rather than phylogenetic diversity in a marine fish assemblage

Josette Cachera

V.1 Introduction

Facing the rate of species loss, there is a growing interest in ecosystem functioning and in whether diversity may be involved in ecosystem properties, e.g. stability. It is now well recognized that ecological processes and ecosystem functioning are not driven by taxonomic diversity but rather by functional diversity, i.e. the diversity of ecological functions performed by species (Loreau 2000; Wardle *et al.* 2000; Hooper *et al.* 2005; Petchey & Gaston 2006). A critical point to assess functional diversity is to choose traits that are relevant to characterize species ecological functions, also known as functional traits (Scherer-Lorenzen 2005; Petchey & Gaston 2006).

Energy transfer and nutrient cycling is one of the main ecosystem processes and species functions related to food resource use are therefore critical. In animal ecology, morphological attributes of the feeding apparatus have often been chosen as functional traits to characterize the trophic function of species (Wainwright *et al.* 2004; Bellwood *et al.* 2006). Yet, instead of focusing on particular morphological features related to only one function, such an approach may be improved by using the whole body shape of animals as it is supposed to integrate many other ecological functions such as sediment removal or dispersion by a particular type of locomotion (Farré *et al.* 2013). This reasoning is based on the idea that body shape constrains movements of organisms, their interactions with the environment (both biotic and abiotic), and their ability to perform ecological functions as developed in the field of ecomorphology. Several authors already hypothesized that body shape taken as a whole may indicate the ecological position of species, e.g. in stream fishes (Gatz 1979) or in birds (Ricklefs & Travis 1980; Ricklefs 2012); by extent, morphology is generally related to species ecological function and functional ecology (Motta *et al.* 1995; Norton *et al.* 1995; Albouy *et al.* 2011; Price *et al.* 2011).

According to the niche diversification principle (West-Eberhard 1989), structurally complex habitats are supposed to promote functional diversification and thus morphological diversification if morphology is actually related to function. In case of adaptive radiation, it is expected that phylogenetic distance between species is related to functional and morphological diversity (Srivastava *et al.* 2012). However, it is also possible that phylogenetically unrelated species exhibit close functions and morphologies because of evolutive convergence. In such case, no relationships between phylogenetic distance and functional diversity is expected (Devictor *et al.* 2010). Alternatively, the environment could filter species along time so that only similar species coexist regardless of their phylogenetic relationship. Such niche filtering would thus imply that functional and morphological diversity are not related to phylogenetic distance (Zobel 1997). In view of the above hypotheses, it appeared central for efficiently measuring functional diversity to make clearer the relationships between phylogeny, morphology, and function.

Besides diversity across species, individual variability has also consequences for ecosystem functioning. It is now well appreciated that conspecifics are not equivalent, and that intra-specific variation impacts community organization (Bolnick *et al.* 2003, 2011). It seems coherent indeed to hypothesize that individuals may vary in terms of morphology, performance (fitness), and maybe function (West-Eberhard 1989; Cianciaruso *et al.* 2009; Albert *et al.* 2012). Given the difficulty of directly assessing an individual’s function, one way to study functional variability between conspecific would be to measure individual morphological variability. Further, following the Niche Variation Hypothesis (NVH, Van Valen 1965), which states that a broader ecological population niche allows greater individual variation, it may be expected that species niche breadth is positively related to morphological variability between conspecifics, and thus to individual functional variability.

Some ecological functions necessitate extreme morphological specialization, which also generally implies particularly low morphological and functional variability between conspecifics (a hypothesis referred to as the Specialization-Variability Hypothesis, SVH, thereafter). Functional identity (i.e. the set of functional traits of an organism) may thus be related to species ecological niche characteristics, i.e. species specialization (or niche position), niche breadth and individual variation, and species specialization is expected to be negatively related to both niche breadth and individual variation. Such relationship may, however, be blurred in some taxa. Fish, for example, exhibit very diverse morphologies, but are also known to be ecologically versatile (Bellwood *et al.* 2006; Albouy *et al.* 2011). It results that, whatever their apparent degree of morphological specialization, be it at the species or individual level, they exhibit wide variation in trophic behaviours (Albouy *et al.* 2011) and perform a diversity of ecological functions (Liem & Summers 2000; Bellwood *et al.* 2006; Albouy *et al.* 2011). Fish are thus a powerful model taxon to assess the links between phylogeny, morphology and functional identity across species if any, and to test whether niche characteristics, particularly niche breadth and individual variability, are related to functional identity.

The aim of this study was to investigate whether morphology and/or phylogeny are related to ecological function and how niche characteristics covary, using an assemblage of 11 teleost fish species of the eastern English Channel as a case study. We used morphological space as a representation of ecological space and extracted individual morphological characteristics using Procrustes analysis, a geometric morphometric method that allows to compare shapes based on the superimposition of morphological landmark configurations (see Adams *et al.* 2004; Slice 2007 for reviews). We investigated first the links between phylogeny, morphology and functional identity across species, and then evaluated relationships between niche characteristics, namely species morphological niche specialization, individual morphological variation, and species niche breadth. It was hypothesized that (i) phylogeny is related to species morphology; (ii) species morphology, and thus phylogeny, should be associated with species functional identity; (iii) the NVH holds in the assemblage, i.e. niche breadth is positively related to individual variation, as well as the SVH, i.e. species specialization is negatively related to niche breadth and individual variation; and (iv) these correlations between niche characteristics may be related to functional identity.

V.2 Materials and methods

V.2.1 Sample collection

Eleven species of teleost fish (**Table V.1**), chosen for the diversity of their habitats and morphology, were collected in the eastern English Channel during the Channel Ground Fish Survey (CGFS) operated by IFREMER in October 2009 (**Fig. V.1**). Fish were caught on board RV "Gwen Drez" by towing a high opening demersal trawl (GOV) with a cod-end of 10 mm stretched mesh for 30 minutes at a speed of approximately 3.5 knots. A spatially stratified sample scheme was used, the area being subdivided into 15' x 15' rectangles in which the GOV trawl was fished at least once. For each species, all sizes were sampled. Following the capture, species were identified and individuals were labelled, frozen on board with liquid nitrogen and kept frozen until further use.

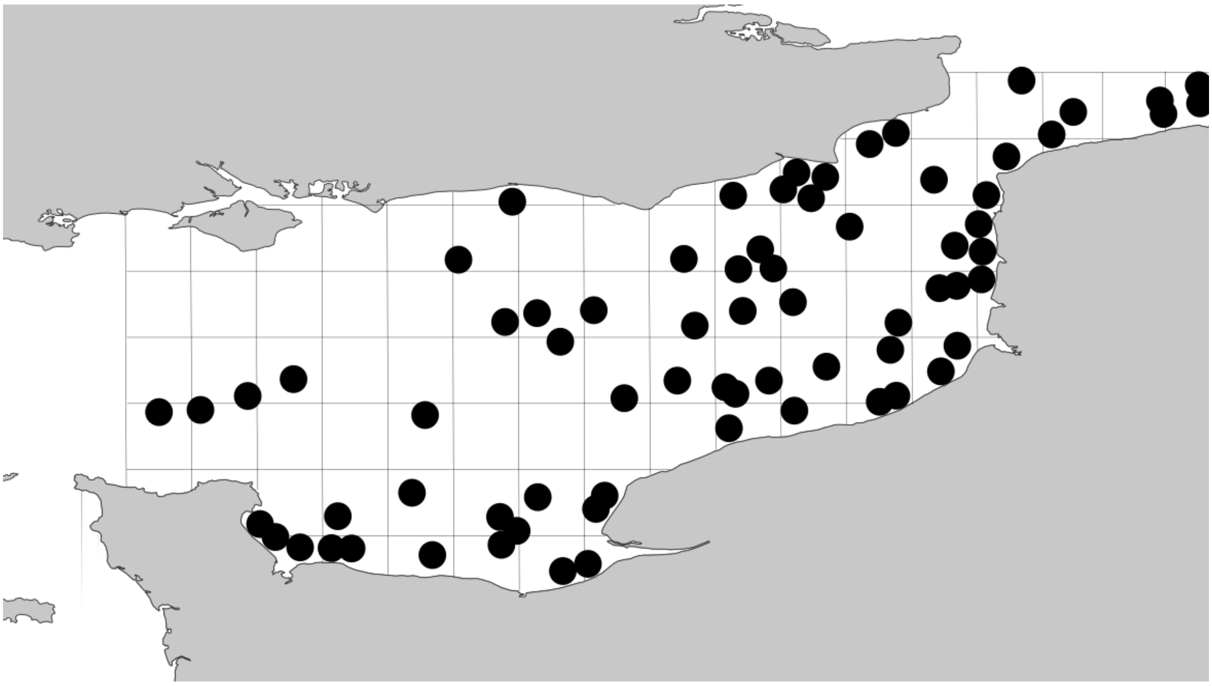


Figure V.1: Map of the area covered by the Channel Ground Fish Survey with sampling points (trawls' location). Only trawls that captured fish used in this study are represented.

V.2.2 Morphometrics

In the laboratory, the fish were defrosted. A numerical picture of each fish was taken with a camera (Nikon® D7000) positioned at 140 cm height using a Kaiser® camera stand. 22 landmarks and semi-landmarks along the whole body were captured from the picture using

ImageJ® (**Fig. V.2**; see **PhD ANNEXE 2** for a precise description of (semi-)landmarks). (Semi-)Landmarks were chosen to describe the principal characteristics of fish body shape and were homologous, i.e. common to all species and individuals. Landmarks (points 1 to 3, 7 to 13, and 17 to 22; **Fig. V.2**) corresponded to anatomical features and semi-landmarks (points 4 to 6 and 14 to 16; **Fig. V.2**) were constructed by dividing the individual's standard length in quarters. A Generalized Procrustes Analysis (GPA) was performed on (semi-)landmark coordinates taken as morphological data (Goodall 1991; Rohlf & Marcus 1993; Dryden & Mardia 1998). GPA scales, translates and rotates individual (semi-)landmarks' configurations so as to minimize the sum of squared distances between pairs of homologous (semi-)landmarks (superimposition). The distances between individual (semi-)landmarks after superimposition and the resulting mean landmark configuration are called Procrustes residuals and represent individuals' position in the assemblage morphospace. Coordinates of the mean landmark configuration of each species were then used in a hierarchical clustering, using Euclidean distance and average method (Legendre & Legendre 1998) in order to depict the morphological tree and assess morphological groups of species.

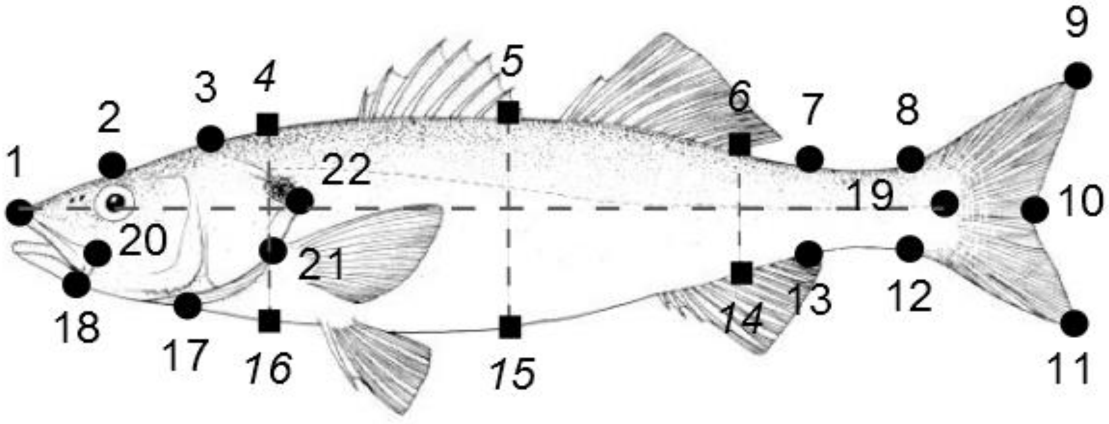


Figure V.2: Location of homologous landmarks (filled circles, points number 1 to 3, 7 to 13, and 17 to 22) and semi-landmarks (filled squares, points number *4 to 6* and *14 to 16*) used to describe individual fish body shape. European seabass (*Dicentrarchus labrax*) is presented as an example but the same (semi-)landmarks were used for all species.

We simplified the representation of the assemblage morphospace by performing a Principal Components Analysis on individual Procrustes residuals of all species (traditionally called Relative Warps Analysis, RWA, in geometric morphometrics, Adams *et al.* 2004) in order to identify potential morphological units within the assemblage. The RWA was completed by calculating deformation grids along the RWA axes that allowed to consider changes in (semi-

)landmark configuration relative to the mean body shape along these axes. Histograms of the distribution of individuals along each axis of the RWA were also produced in order to identify the source of variability (inter- and/or intra-specific) was described by each axis. Two morphological niche characteristics were then extracted for each species (**Table V.1**). A species' morphological specialization was estimated by the distance between the centroid of the species' morphological niche position and the centroid of the assemblage morphospace in the RWA (MD, **Table V.1**), considering that the larger this distance, the more specialized is the species' morphology (Bellwood *et al.* 2006). Individual morphological variation was estimated as the mean distance of individuals to the centroid of their species morphological niche (V , **Table V.1**). All analyses were performed with the package "shapes" (Dryden 2012) of the software (R Core Team 2012).

V.2.3 Assessing species niche breadth

Given the implication of morphology for trophic functions, we decided to use a measure of species niche breadth based on trophic niche. Fish were dissected to extract their digestive tract and the contents removed and kept in Petri dishes for analysis. Prey were identified to the lowest possible taxon under a stereo microscope Olympus SZX16©, sorted, counted and weighed (0.1 g) in non-empty digestive tracts. Prey items were then grouped in 41 categories combining taxonomic level and functional characteristics (see **PhD ANNEXE 3** for a complete description of prey categories). Then, for each fish species, the proportion p_{ij} of each prey category i in the diet was calculated on the basis of the Geometric Mean (GM) of prey number and weight such as:

$$p_{ik} = \frac{\sqrt{W_{ik} \times N_{ik}}}{\sum_{i'} (\sqrt{(W_{i'k} \times N_{i'k})})} = \frac{g_{ik}}{\sum_{i'} g_{i'k}},$$

where W_{ij} and N_{ij} are the total weight and the total number of prey categories i in the diet of focal fish species j, respectively. We used GM to calculate prey category proportion in the fish's diet as a new index to compensate for prey importance in weight and number. Combining these two aspects is considered effective in depicting dietary importance of prey categories, since it allows us to take into account energy consumption (prey biomass, W_i) and foraging behaviour (prey count, N_i) (see Hyslop 1980 for discussion). Trophic niche width was determined for each species using Levin's index,

$$B_j = \frac{1}{\sum_i {p_{ij}}^2},$$

which tends to 0 when the species has a narrow niche breadth (feeds only on one prey category) and increases with niche breadth (increasing diversity of food resources, Levin 1968).

Table V.1: Studied species and their morphological niche characteristics. Species scientific and common names, sample size (n). MD (niche distance to species assemblage morphospace's centroid) representing species morphological specialization V (mean individual distance to species centroid) representing individual variability, and B_j the index of Levin representing the species trophic niche breadth.

Scientific name	**common name**	**n**	**MD (cm)**	V	B_j
Chelidonichthys cuculus	red gurnard	42	17.3	4.02	5.78
Chelidonichthys lucerna	tub gurnard	51	18.7	4.44	6.53
Merlangius merlangus	whiting	61	16.9	3.61	4.92
Gadus morhua	cod	37	15.6	2.50	10.20
Trachurus trachurus	horse mackerel	87	8.2	4.39	4.51
Sprattus sprattus	sprat	41	15.7	3.05	1.59
Sardina pilchardus	pilchard	39	19.0	4.03	1.18
Clupea harengus	herring	32	17.1	3.38	2.62
Scomber scombrus	mackerel	61	21.3	2.24	4.62
Mullus surmuletus	surmullet	101	28.4	4.08	5.29
Dicentrarchus labrax	seabass	87	18.4	2.85	7.19

V.2.4 Phylogeny

To assess phylogenetic relationships between fish species, the entire DNA sequence of mitochondrial Cytochrome-*b* (1140 base pairs) was extracted from the *GenBank® database* for each species (Benson *et al.* 2000). Cytochrome-*b* sequence is commonly used in phylogenetic and evolutionary studies in several groups of organisms (e.g. fish, Cespedes *et al.* 1998; Dowling *et al.* 2002) and is recognized as the most useful DNA sequence to determine phylogenetic relationships between organisms (Branicki *et al.* 2003). The cytochrome-*b* sequences of all fish species were then aligned and a phylogenetic tree was computed using a maximum-likelihood algorithm (Dereeper *et al.* 2003). A matrix of phylogenetic distances between species was extracted from the phylogenetic tree and used to identify phylogenetic groups of species. The matrix was then decomposed in principal components (phyloPC), a subset of which was selected by the broken stick model (Diniz-Filho *et al.* 1998) for further analyses.

V.2.5 Functional traits

Nine functional traits, either qualitative or quantitative, were extracted from Fishbase (Froese & Pauly 2013) for each species. These were the species' place in the water column, swimming mode, foraging strategy, usual depth, habitat, foraging behavior at juvenile and adult stages, foraging time and trophic level (**Table V.2**). As advised by Legendre & Legendre (1998) and Petchey & Gaston (2002), a hierarchical clustering, using Gower's distance and the average method, was used to compute a functional tree and thus assess functional groups of species.

Table V.2: Species functional traits, i.e. place in the water column (Water), swimming mode (Swim), foraging strategy (Forage), usual depth (Depth), usual habitat (Habitat), foraging behavior of young (Young) and adult (Adult), foraging time (Time) and trophic level (TL). NA = Non Available.

Species	**Water**	**Swim**	**Forage**	**Depth**	**Habitat**	**Young**	**Adult**	**Time**	**TL**
Red gurnard	demersal	subcarangiform	searcher	30-250	shelf	NA	NA	diurnal	3.85
Tub gurnard	demersal	subcarangiform	searcher	20-318	shelf	NA	NA	diurnal	3.65
Whiting	bentho-pelagic	subcarangiform	NA	10-200	all	NA	NA	NA	4.37
Cod	bentho-pelagic	carangiform	NA	0-600	shelf	both	NA	nocturnal	4.42
Horse mackerel	semi-pelagic	carangiform	school	0-200	shelf	school	school	everytime	3.64
Sprat	pelagic	carangiform	school	10-150	NA	school	school	diurnal	3.00
Pilchard	pelagic	carangiform	school	25-100	coastal	school	school	NA	3.05
Herring	pelagic	carangiform	school	0-200	all	school	school	diurnal	3.23
Mackerel	pelagic	carangiform	school	0-200	shelf	school	school	diurnal	3.65
Surmullet	demersal	subcarangiform	searcher	5-60	NA	NA	NA	NA	3.42
Seabass	demersal	subcarangiform	NA	10-100	coastal	alone	school	diurnal	3.79

V.2.6 Statistical analyses

Firstly, pairwise comparisons of the topology of the three trees (phylogenetic, morphological, and functional) were performed using the contingency table approach (Borcard *et al.* 2011). It tests the relationships between two topologies using a χ^2 test, and performed Monte Carlo simulation assess its significance. See **Fig. V.3** for analytical procedure. When the test is significant, topologies are considered similar and trees significantly equivalent. Redundancy Analyses were then performed as *post-hoc* tests to assess the proportion of variance in the mean body shape of species (mean Procrustes residuals) explained by phylogeny using phyloPC as explanatory variables (Desdevises *et al.* 2003) on the one hand and by functional identity using functional group membership as the explanatory variable on the other hand.

Secondly, the NVH and the SVH were tested by computing Pearson correlation tests between species niche characteristics, i.e. species morphological specialization MD, individual morphological variability V and species trophic niche breadth B_j (**Table V.1, Fig. V.3** for analytical procedure.). A positive relationships was expected between B_j and V, following the NVH, and negative relationships were expected between MD and B_j and between MD and V following the SVH.

Finally, in order to detect if species niche characteristics were related to species functional identity, ANOVAs were performed on morphological niche characteristics with species membership to a functional group as explanatory variable. See **Fig. V.3** for analytical procedure.

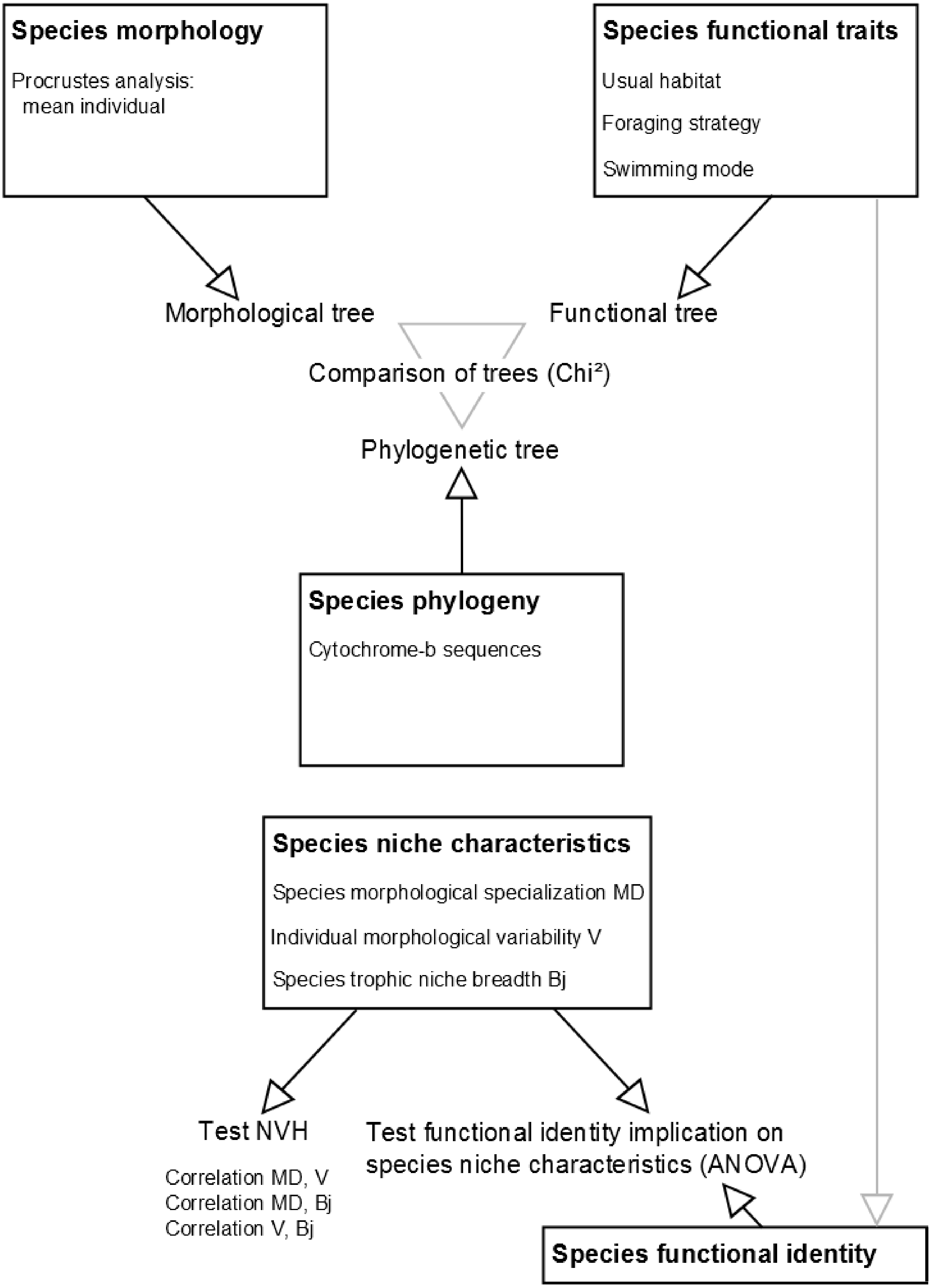


Figure V.3 : Scheme of analytical strategy.

V.3 Results

The 3 first axes of the Relative Warps Analysis (RWA) explained 72.71% of total variation versus only 62.47% for the 2 first axes, and were thus all kept in the analysis. Five morphological units were identified: three groups of species, namely gurnards (group 1), gadoids, i.e. whiting and cod (group 2), and small pelagics, i.e. mackerel, horse mackerel and clupeid fishes (group 3; **Fig. V.4 a**), plus two isolated species, surmullet and seabass, that were separated from the three groups along axis 1, which explained 50.67% of the total variation. Axis 2, which explained 11.8% of total variation, discriminated group 1 from the others. Axis 3, which accounted for 10.23% of total variance, allowed to distinguish group 2 from group 3. Deformation grids that describe morphological changes along the 3 RWA axes showed that positive values along axis 1 corresponded to shorter body, along axis 2 represented square-shaped heads, and along axis 3 indicated shorter and thinner caudal peduncle and more fusiform body shape (**Fig. V.4 b**). Histograms of the distribution of individuals along axes of the RWA confirmed that surmullet and seabass were discriminated from the other species along axis 1, red and tub gurnards (group 1) along axis 2 and gadoids (group 2) along axis 3. No single axis allowed to distinguish small pelagics (group 3) from the others, the combination of the 3 axes being necessary (**Fig. V.4 a**). No axis allowed to identify intra-specific morphological sub-units (**Fig. V.4 c**). Groups of species were therefore morphologically different enough relative to intra-specific variability in order to be used as trustworthy morphological units.

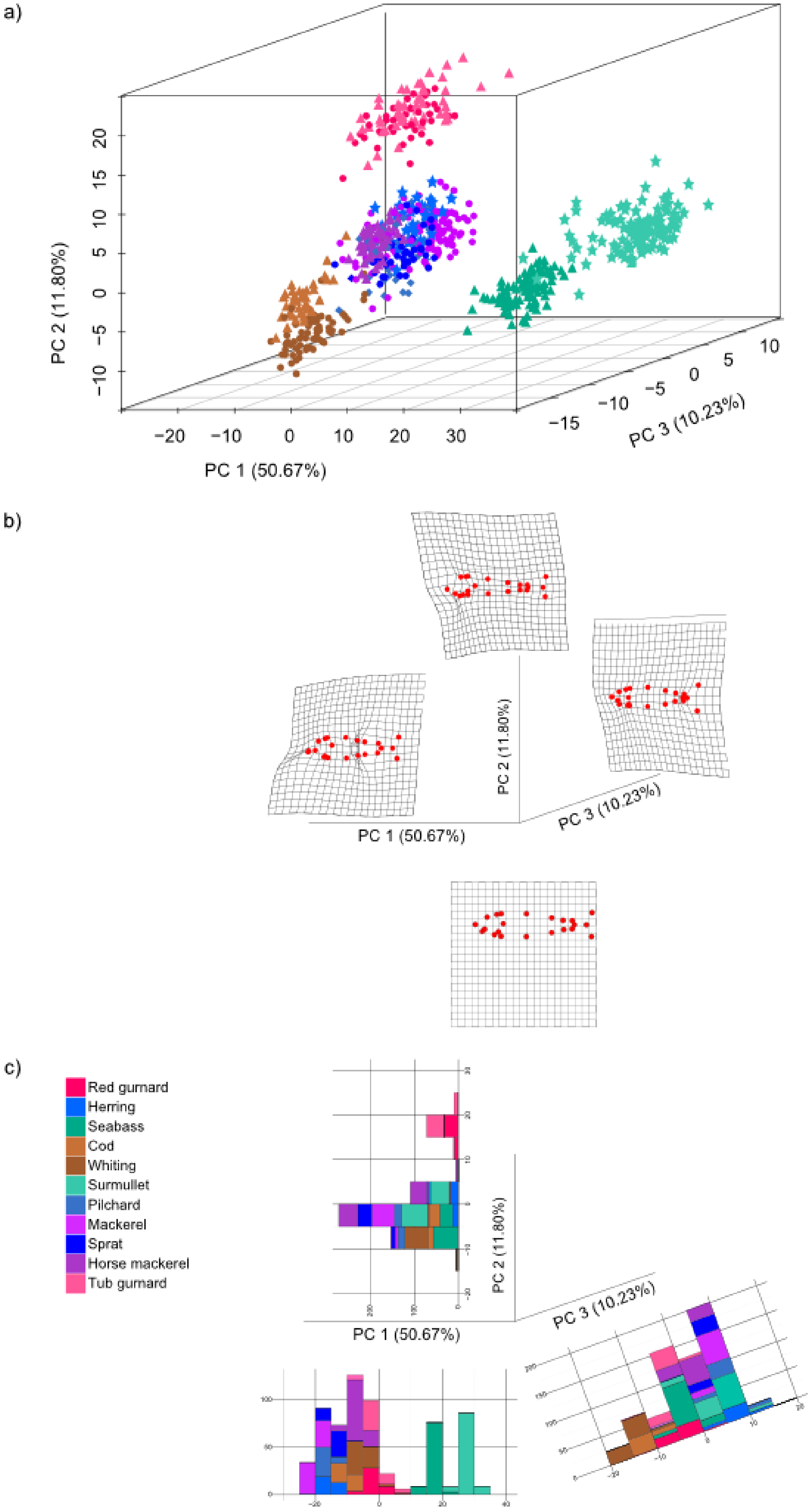

a)
PC 1 (50.67%)
PC 2 (11.80%)
PC 3 (10.23%)
−20 −10 0 10 20 30
−10 −5 0 5 10 15 20
−15 −10 −5 0 5 10
b)
PC 1 (50.67%)
PC 2 (11.80%)
PC 3 (10.23%)
c)
Red gurnard
Herring
Seabass
Cod
Whiting
Surmullet
Pilchard
Mackerel
Sprat
Horse mackerel
Tub gurnard
PC 1 (50.67%)
PC 2 (11.80%)
PC 3 (10.23%)

Figure V.4: Species' morphological niche in assemblage morphospace. a) Relative Warps Analysis (RWA) representing the species assemblage morphospace and b) d'Arcy Thompson's deformation grids describing changes in body shapes along the three axes describing assemblage morphospace. c) Histograms of the distribution of individuals along each axis of the RWA. Numbers in parentheses are percentages of variance explained by the first 3 principal components. 95% equal frequency ellipsoid are not represented for readability purpose. Red gurnard (pink circle), tub gurnard (pink triangle), surmullet (green triangle), seabass (green star), whiting (brown circle), cod (brown triangle), horse mackerel (purple circle), pilchard (blue diamond), sprat (blue circle), herring (blue star), mackerel (purple triangle).

The phylogenetic tree was neither significantly related to the morphological tree calculated on the basis of the morphospace (χ^2 = 10.08, P-value = 0.48), nor to the functional tree (χ^2 = 8.25, P-value = 0.26), whereas the morphological tree and the functional tree were strongly related (χ^2 = 22, P-value = 9.99e-04, **Fig. V.5**).

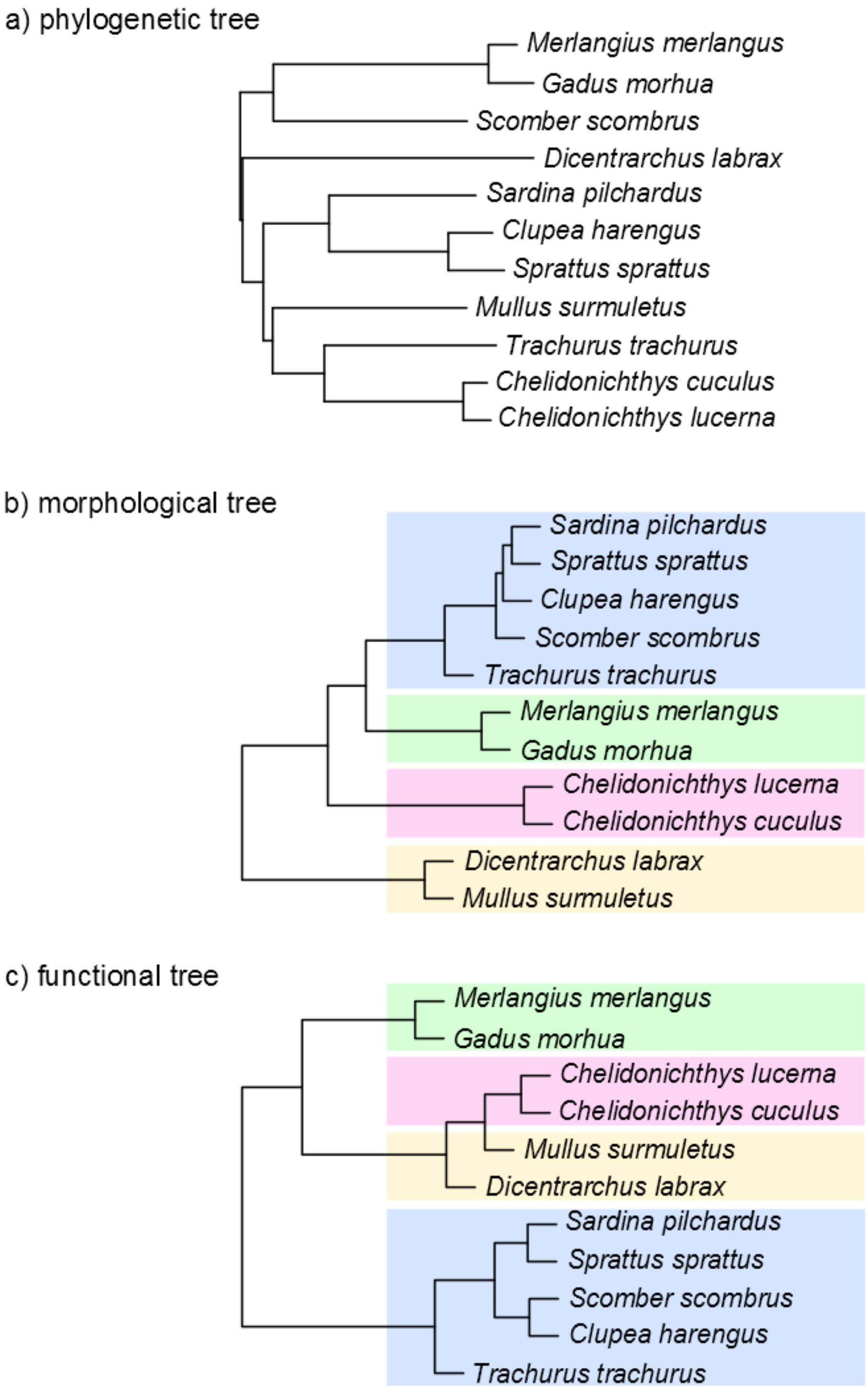


Figure V.5: Clustering of the studied species according to phylogenetic, morphological and functional relationships. a) phylogenetic tree, b) morphological tree, c) functional tree.

The morphological and the functional tree depicted the same four groups of species (**Fig. V.4 b & c**). These groups can be qualified as (i) schooling pelagic feeders (pilchard, sprat, herring, mackerel and horse mackerel), (ii) shelf demersal feeders (red and tub gurnards), (iii) higher omnivores (cod and whiting), and (iv) coastal demersal feeders (seabass and surmullet, **Fig. V.5 b & c**).

There was no significant phylogenetic signal detected in morphological variation across species although 28.94% of variance was explained (*P*-value = 0.76), whereas functional identity appeared to be significantly involved in morphological variation across species explaining 27.83 % of variance (*P*-value = 0.04).

None of the expected correlations, i.e between species trophic niche breadth B_j and individual morphological variability V according to the NVH and between species morphological specialization MD and both B_j and V according to the SVH, were significant (**Table V.3**). In the same manner, none of the ANOVAs on niche characteristics (MD, B_j & V, **Table V.3**) explained by species membership to a functional group was significant (**Table V.3**).

Table V.3: Relationships between species niche characteristics and functional identity. Pearson correlation tests between three species niche characteristics, i.e. species trophic niche breadth B_j, species morphological specialization MD, and individual morphological variability V are presented as well as results of ANOVAs on species niche characteristics explained by species membership to functional group.

Hypothesis	**Model**	**P-Value**	**Cor**
NVH			
	$MD \sim B_j$	0.9688	0.01
	$MD \sim V$	0.8197	-0.08
	$B_j \sim V$	0.4732	-0.24
Functional affiliation			
	MD ~ functional group	0.368	
	B_j ~ functional group	0.070	
	V ~ functional group	0.368	

V.4 Discussion

Our study showed that inter-specific morphological similarity was not associated with phylogenetic proximity but rather with functional proximity in an assemblage of eleven marine fish species. In addition, intra-specific morphological variability was not related to species trophic niche breadth contrary to the Niche Variation Hypothesis and both were unrelated with species morphological specialization contrary to the Specialization-Variability Hypothesis. This suggests that functional identity does not constrain species niche, which was confirmed by the absence of relationship of intra-specific morphological variability, trophic niche breadth and species morphological specialization with species functional group. It has been recently pointed out that ecological studies need to focus on multiple species and/or trophic levels (Bolnick *et al.* 2011) and our results clearly support this point by highlighting the complex organization of the fish assemblages and revealing a discrepancy between taxonomical and functional diversity.

V.4.1 Phylogeny and body shape

Contrary to our first assumption, it was established that the diversity of body shapes across species was not linked to phylogeny as phylogenetic groups mismatched morphological groups and morphological variation was not significantly related to phylogenetic distance. Notice however that 30 % of morphological variation across species was explained by phylogenetic distance despite non significance. The hypothesis of evolutive convergence, which states that species experiencing similar environmental conditions would evolve towards similar phenotypic traits among which morphology, could explain these results. Cases of fish community composition resulting from evolutive convergence were both described in the literature (Gatz 1979; Winemiller 1991; Kocher *et al.* 1993; Winemiller *et al.* 1995). Our fish community was composed of four morphological groups that were located in different places of the assemblage morphospace and did not overlap (**Fig. V.4**), implying that they had very distinct body shapes. Two of these groups were composed of phylogenetically related species, red gurnard and tub gurnard (genus *Chelidonichthys*) for the first one and whiting and cod (family gadidae) for the second. The other two groups included clupeid fish (family clupeidae) associated with mackerel (family scombridae) and horse mackerel (family carangidae) on the one hand and seabass (family moronidae) and surmullet (family mullidae) on the other hand, that is fish species with similar body shapes although phylogenetically unrelated. It may be hypothesised that such configuration is resulting from evolutive convergence, implying relatively close ecological and functional niches (Cadotte *et al.* 2013).

V.4.2 Body shape and function

In line with the field of functional ecology that points out that biodiversity should be assessed through functional diversity rather than taxonomical diversity (Loreau 2000; Loreau *et al.* 2001), phylogenetic groups of species were not related to functional groups. Four functional groups of species, corresponding perfectly to the morphological groups previously identified, could be determined: shelf demersal feeders (red and tub gurnards), higher omnivores (cod and whiting), schooling pelagic feeders (pilchard, sprat, herring, mackerel and horse mackerel), and coastal demersal feeders (seabass and surmullet).

The composition of these functional groups in terms of species may be explained by habitat characteristics following the theory of niche filtering, which states that environmental factors act like filters for niche so that coexisting species tend to be particularly similar in terms of niche, traits, and function whatever their taxonomy (Zobel 1997). This hypothesis appears as complementary to the evolutive convergence hypothesis previously mentioned to explain the absence of link between phylogeny and both morphology and functional identity.

The composition of the assemblage itself in terms of functional groups may be explained by niche diversification (West-Eberhard 1989) following the idea that environmental complexity promotes ecological diversity (Schluter 1996; Price *et al.* 2011). First, the pelagic environment being less diverse than the benthic one (Gray 1997), it is expected that pelagic species exhibit less diversity in terms of morphological and ecological characteristics than demersal or benthic species. In agreement with this expectation, pelagic species from this study belonged to the same morphological and functional group, revealing strong functional redundancy and probably similar ecological niches. These species almost certainly experience common biotic and abiotic conditions, due to their position in the water column (homogeneous pelagos), and have similar lifestyles, such as living in school and being highly mobile (Gerlotto & Paramo 2003; Godo *et al.* 2004). In this case, niche filtering may apply at the scale of the whole pelagic environment and may thus explain morphological similarity and functional redundancy between pelagic species. In contrast, demersal and bentho-demersal species were more dispersed in the species assemblage morphospace and belonged to contrasted morphological and functional groups. Since the benthic environment is recognized as being particularly diverse due to a mosaic of habitats, especially in continental shelf seas such as the eastern English Channel (Anorve-Sanvicente *et al.* 1996; Foveau *et al.*

2013), it is expected to promote niche diversification where species, or group of species as in our case, tend to be functionally complementary to avoid ecological competition (competitive exclusion). In this case, niche filtering may apply at the scale of the different benthic habitats thus explaining that, although they roughly share the same position in the water column, bentho-demersal species (gurnards) and demersal species (cod and whiting on the one hand, and seabass and surmullet on the other hand) composed 3 different morphological and functional groups.

In conclusion, along the debate about the implication of species diversity in functional diversity (Loreau *et al.* 2001; Hooper *et al.* 2002, 2005), our results suggest that (i) the functional composition of communities and the resulting functional and/or niche diversity depends on environmental heterogeneity, and that (ii) the taxonomic composition of functional groups is driven by niche filtering in common environmental conditions or common habitat.

V.4.3 The Niche Variation Hypothesis and functional attribution

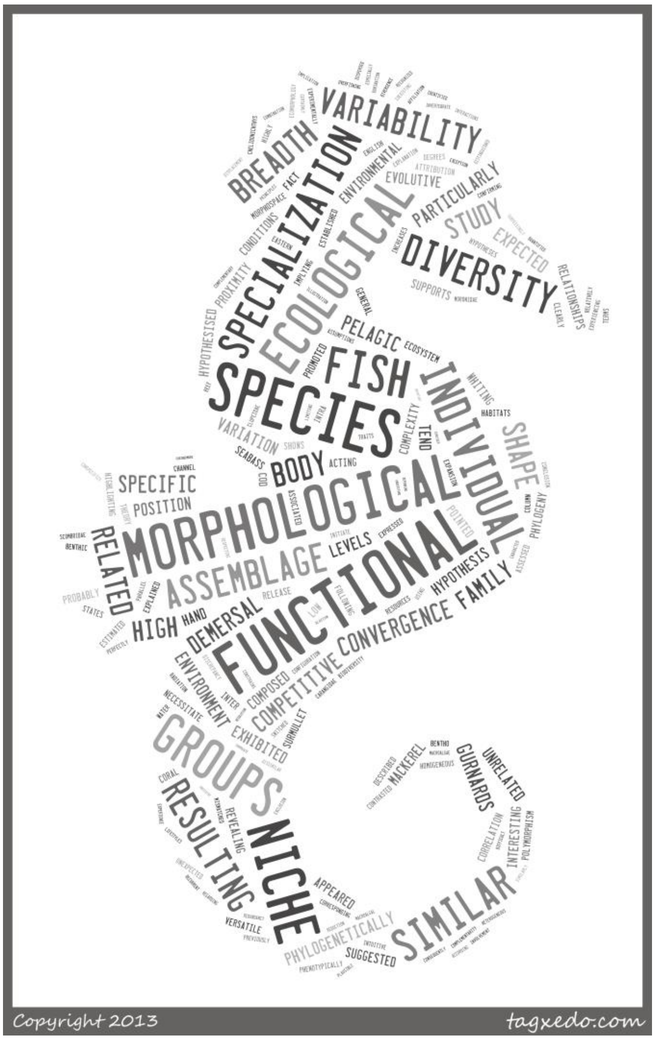
Contrary to the Niche Variation Hypothesis (Van Valen 1965) and the Specialization-Variability Hypothesis, characteristics of species niches within the assemblage appeared unrelated. More specifically, species trophic niche breadth and individual morphological variation were not correlated nor were they with different degrees of morphological specialization (morphological niche position). These results were unexpected as one may predict several correlations between these characteristics related to the effect of competitive pressures. Strong inter-specific competition is indeed supposed to (i) induce phenotypic divergence between species, according to the principles of competitive diversification and ecological character displacement (Schluter 2000; Svanbäck *et al.* 2008), and to (ii) promote niche contraction and phenotypic convergence between conspecifics in order to mitigate competitive interactions with individuals from other species. Consequently, high species morphological specialization would imply narrow niche and weak individual variation (SVH) and broad niches should be associated with large individual variation (NVH). Several explanations can be proposed for the absence of all or part of these relationships. First, it may be possible that resources are not limiting such that current competition is relaxed in the assemblage and the expected relationships between niche characteristics cannot be observed. Second, species trophic niche breadth may be an irrelevant measure of ecological niche breadth. However, there is no easy measure of species ecological niche and the relationship between species trophic niche breadth and individual morphological variation was already shown to support the NVH (in passerine birds, Hsu *et al.* 2013). Testing the NVH using trophic niche breadth and individual morphological variation implies assuming a link between diet and morphology, an assumption that is still debated for fish. Previous studies found no or weak, but significant, relationships between diet and morphology in fish (Douglas & Matthews 1992; Labropoulou & Markakis 1998; Svanbäck & Eklöv 2003; Ibañez *et al.* 2007; Bolnick & Paull 2009). It may be possible that the NVH cannot be supported by combining trophic niche and morphological variation in fish because of a lack of link between diet and morphology in this taxon.

V.4.4 Species niche and functional identity

The characteristics of species niches (species morphological specialization, trophic niche breadth and individual morphological variability) appeared unrelated to species functional identity. We initially expected that different ecological functions would necessitate varying degrees of morphological specialization and be negatively related individual morphological variability. It was particularly unexpected that species belonging to the schooling pelagic feeder group, which were morphologically similar, did not exhibit particularly high specialization of body shape nor weak individual variability. Choosing relevant functional traits is a recurrent issue in functional ecology (Scherer-Lorenzen 2005; Petchey & Gaston 2006), and given that we used only 10 functional traits, the illustration of the ecological functions performed by the studies species may have been too imprecise. It may also be hypothesised that the functions performed by these species do not necessitate particularly high morphological specialization or that fish are functionally versatile enough to perform similar functions with dissimilar morphologies. It is difficult to evaluate the respective contributions of these two options but a combination of both appears plausible. Because of their functional versatility, fish may tend to perform functions that do not required high specialization. Conversely, even fish species with highly specialized body shape can change functional identity. In an interesting study, (Bellwood *et al.* 2006)highlighted that a coral reef fish species could switch function from invertebrate and plankton feeder to macroalgal remover. This species expressed this new function after an experimental shift from a coral to a macroalgae dominated ecosystem to simulate overfishing and was thus able to initiate the recovery of the coral reef. The authors described this functional switch as an “ecological surprise” and named this ability to perform a new function as a “sleeping functional group”. In line with this conclusion, it could be hypothesised that even if fish morphology is an indicator of the general or usual ecological functions they perform, the relationship between morphology and function is not strictly a one-to-one mapping due to their functional versatility.

V.4.5 Conclusion

The present work demonstrates the interest of using the whole body shape as a surrogate of functional ecology, as suggested by others (e.g. Ricklefs 2012). An assemblage of eleven marine fish species from the eastern English Channel revealed an organization depending weakly on phylogeny but rather on morphology and functional identity, that appeared to be themselves related to environmental complexity. Furthermore, our results support the idea that functional groups might be a better level of organization than species to understand community organization. It would be interesting to consider other communities and/or ecosystems in order to assess the generality of our results, but they suggest that it is necessary to consider at least four different levels of organization when studying natural community: the whole community itself, functional groups, species, but also individual characteristics, which might matter for species relationships and functions performed in the ecosystem.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Chapter VI Intra- and inter-specific determinism of trophic relationships in a fish community

Josette Cachera

VI.1 Introduction

A fundamental goal in ecology is to describe and understand intra- and inter-specific interactions (Sutherland *et al.* 2013). Trophic interactions or predator-prey relationships in particular were often studied because of their primary importance in shaping community and ecosystem functioning. Competition for food resources, whether it is intra- or inter-specific, influences population and community dynamics and promotes niche diversification and specialization by competitive exclusion (Svanbäck & Bolnick 2008; Albouy *et al.* 2011). Trophic interactions also play a major role in ecosystem functioning since they mediate one of the main processes in ecosystems, i.e. energy and biomass transfer across food web, and are particular pathways for perturbation propagation across communities through trophic cascades (McCann *et al.* 1998; Rooney *et al.* 2006). Identifying the determinants of trophic interactions is therefore a major step towards understanding factors influencing food web structure and dynamics and thus ecosystem functioning.

Basically, trophic interactions take place at the individual level and can be depicted by individual diet variation. The framework of Optimal Foraging Theory (OFT) suggests several determinants of individual diet. OFT assumes that an individual will choose to consume a food resource in order to maximize benefits such as energy intake against costs that range from foraging and handling time to digestion energetic costs and exposition to predators (Werner & Hall 1974). Consequently, the main determinants of individual diet can be categorized into exogenous factors, i.e. independent from the individual, and endogenous factors, i.e. depending on the individual. One of the main exogenous factors is prey availability, since it is intuitive that an individual will forage only on prey it encounters in its environment (Ferry-Graham *et al.* 2002), but prey traits and abundance as well as the presence and abundance of competitors or predators are important exogenous factors. Since these are clearly related to habitat, variation in habitat will affect individuals' diet when they are not strict specialists (Svanbäck & Eklöv 2002). Endogenous factors are mainly related to the consumer's phenotype that will affect its feeding requirements and foraging ability. Individual diet can vary according to size due to ontogenetic diet shift (Scharf *et al.* 2000), morphology (Ibanez *et al.* 2007), gender due to sex dimorphism (Bolnick *et al.* 2003), physiological requirements (Bolnick *et al.* 2003; Svanbäck & Bolnick 2008; Araùjo *et al.* 2011)and behaviour, whether it is innate to arising from experience, learning and/or social status (Estes *et al.* 2003). Notice that some of these determinants may be related: different sizes or genders may have different physiological requirement or behaviour for instance.

Despite the numerous studies focusing on one potential determinant, there is a lack of studies that aim at partitioning variation in individual diet between theses factors in order to estimate their relative importance.

Many studies focused on trophic interactions at the species level and tried to identify determinants of species diet or trophic niche. Specifically, the idea that a species is either a generalist (exploiting a wide diversity of food resources) or a specialist (using only a subset of food resources available) depending on its trophic morphology, such as beak shape in birds (Ricklefs 2012) or feeding apparatus morphology in fish (Wainwright & Richard 1995), was developed for decades. Consequently, some authors proposed that morphology may predict species trophic niche (Douglas & Matthews 1992; Wainwright & Richard 1995; Svanbäck & Eklöv 2002; Ibanez *et al.* 2007), following the idea that "the way an organism is constructed influences its ability to interact with its environment" (Wainwright 1991). However, trophic morphology is at least partly genetically coded so that phylogenetic distance between species may be related to trophic morphological distance and thus diet variation across species. Besides this indirect effect on species trophic niche *via* its influence on morphology, phylogeny may also have a direct effect on species diet due to genetically coded feeding behaviour or preferential habitat for example (Best *et al.* 2013). Environmental conditions or habitat also influence species diet directly *via* the same exogenous factors as those mentioned at the individual level and indirectly as they affect phenotype in general and morphology in particular, through phenotypic plasticity. Diet variation across species should thus depend on morphology, phylogeny and habitat directly or indirectly.

Trophic relationships within communities are certainly depending on a combination of all the factors described above (Motta *et al.* 1995; Westneat 1995; Ferry-Graham *et al.* 2002). Therefore, studies of their determinism should combine species- and individual-level considerations and should include the direct and indirect effects of morphology, phylogeny and habitat as well as those of sex, size, physiology, or behaviour. The objective of this study was to identify the determinants of trophic interactions in a natural community of marine fish taken as a case study and to quantify their respective contribution to diet variation at the intra- and inter-specific level. We used stomach content data of 833 individuals from 16 different species to assess individual fish diet. We first developed an intra-specific approach to identify factors implicated in diet variation among conspecifics. We tested whether an individual's diet depended on its morphology, state (maturity stage and size), and habitat within each species separately. It was expected that variation in diet among conspecifics would mainly be explained by variation in individual body size and habitat. In a second step, we developed an inter-specific approach but still based on individual level data. The direct and indirect effects of phylogeny, morphology, individual state (maturity stage, sex and size) and habitat on variation in trophic relationships in the fish assemblage were tested and quantified. It was expected that phylogeny was affecting diet through morphology and that morphology itself was the main determinant of diet variation within the community.

VI.2 Materials & Methods

VI.2.1 Sampling scheme

Sixteen fish species, chosen for the diversity of their trophic habits and morphology, were collected in the eastern English Channel during the Channel Ground Fish Survey (CGFS) operated by IFREMER in October 2009 (**Fig. VI.1**). Fish were caught on board RV "Gwen Drez" by towing a high opening demersal trawl (GOV) with a cod-end of 20 mm stretched mesh for 30 minutes at a speed of approximately 3.5 knots. A spatially stratified sample scheme was used, the area being subdivided into 15' x 15' rectangles in which the GOV trawl was fished at least once (**Fig. VI.1**). Following their capture, focal fish species were identified and individuals were labelled, frozen on board with liquid nitrogen to stop digestion, and kept frozen until further use.

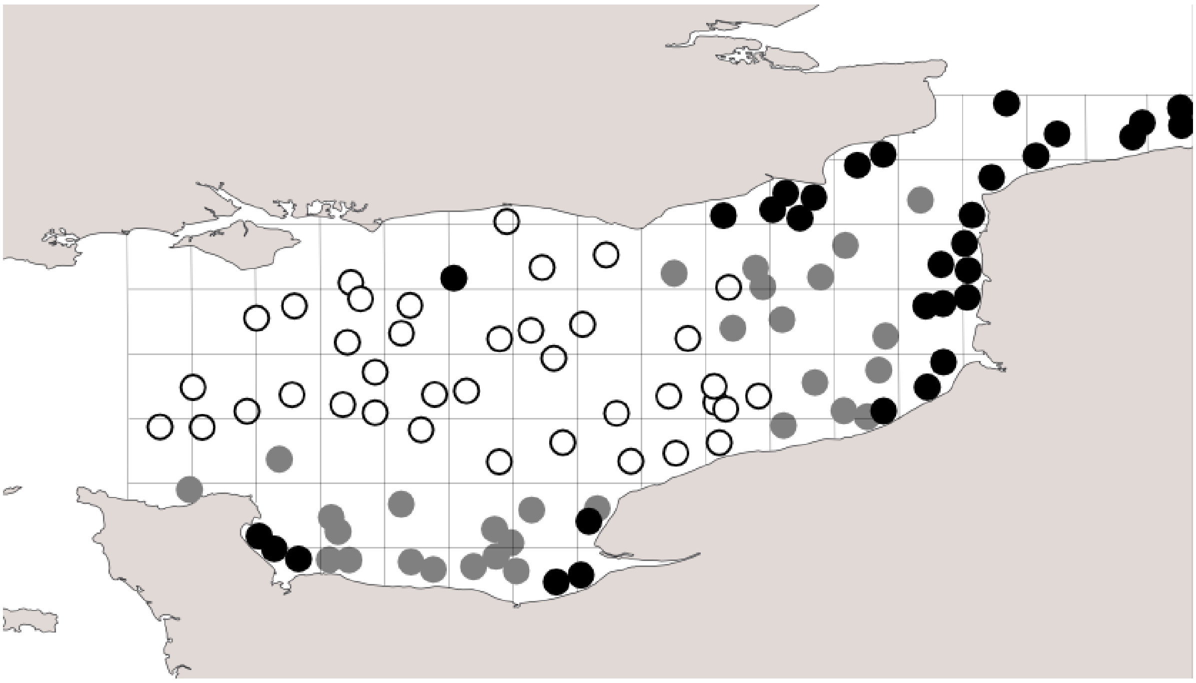

Figure VI.1: Map of the area covered by the Channel Ground Fish Survey with sampling points (trawls' location) and communities defined by hierarchical clustering analysis (see Materials and Methods for details). Each community is characterised by 3 indicator species identified using the index of Dufrêne and Legendre (1997). Community 1 (black circles): *Pleuronectes platessa, Limanda limanda,* and *Merlangius merlangus*; community 2 (grey circles): *Alcyonium digitatum, Sepia officinalis,* and *Mullus surmuletus;* community 3 (open circles): *Loligo forbesi, Spondyliosoma cantharus,* and *Scyliorhinus canicula.*

In the laboratory, the fish were defrosted, measured (total length) and a numerical picture of each fish was taken with a camera (Nikon® D7000) positioned at 140 cm height with a Kaiser® camera stand. 22 landmarks and semi-landmarks along the whole body were captured from the picture using ImageJ® (**Fig. VI.2** and **PhD ANNEXE 2** for a precise description of (semi-)landmarks). (Semi-)Landmarks were chosen to fit the principal characteristics of the whole body shape and were homologous, i.e. common to all species and individuals. Landmarks (points 1 to 3, 7 to 13, and 17 to 22; **Fig. VI.2**) corresponded to anatomical features and semi-landmarks (points 4 to 6 and 14 to 16; **Fig. VI.2**) were constructed by dividing the individual's standard length in quarters.

A Generalized Procrustes Analysis (GPA) was performed on (semi-)landmark coordinates for each species separately. GPA scales, translates and rotates individual (semi-)landmarks' configuration so as to minimize the sum of squared distances between pair of homologous (semi-)landmarks (superimposition). The distances between individual (semi-)landmarks after superimposition and the resulting mean landmark configuration of the species, called Procrustes residuals (hereafter referred to as "intraspecific morphological data", Goodall 1991; Dryden & Mardia 1998), allowed to represent body shape variation among conspecifics within the morphospace of their own species. These were further used in the intra-specific identification of determinants of individual diet variation (see below).

Then, a second GPA was performed on the (semi-)landmark coordinates of all individuals of all species at the same time. The resulting Procrustes residuals, i.e. the distances between superimposed individual (semi-)landmarks and the mean landmark configuration across all species (hereafter referred to as "interspecific morphological data"), allowed to estimate individual variation in body shape in the whole species assemblage morphospace. These were further used for the inter-specific identification of determinants of trophic relationships (see below). All GPAs were performed with the package "shapes" (Dryden 2012) of the software R (R Core Team 2012).

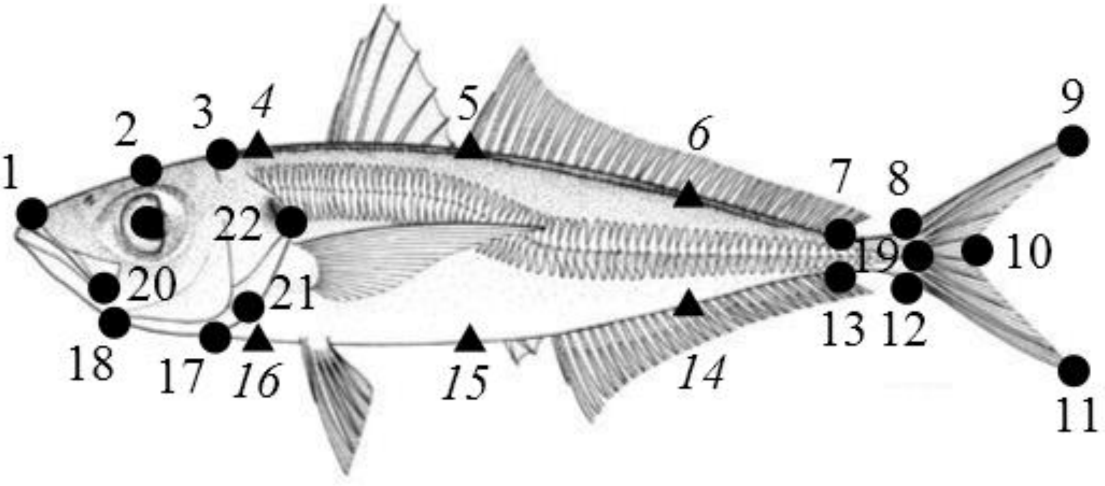

Figure VI.2: Location of homologous landmarks (filled circles, points number 1 to 3, 7 to 13, and 17 to 22) and semi-landmarks (filled squares, points number 4 to 6 and 14 to 16) used to describe individual fish body shape. Atlantic horse mackerel (*Trachurus trachurus*) is presented as an example but the same (semi-)landmarks were used for all species.

VI.2.3 Trophic relationships

Fish were dissected to determine their sex and to extract their digestive tract. The digestive tract contents were spread and kept in Petri dishes for analysis. Prey were identified to the lowest possible taxon under a stereo microscope Olympus SZX16©, sorted, counted and weighed (0.1 g) in 833 available and non-empty digestive tracts corresponding to the 833 individuals used for morphometrical analyses (see above). 96 empty digestive tracts were excluded from analysis. Prey items were then grouped in 41 categories combining taxonomic level and functional characteristics (see **PhD ANNEXE 3** for a complete description of prey categories). Then, for each of the 833 individuals, the proportion p_{ik} of each prey category i in the diet was calculated on the basis of the Geometric Mean (GM) of prey number and weight such as:

$$p_{ik} = \frac{\sqrt{W_{ik} \times N_{ik}}}{\sum_{i'} (\sqrt{(W_{i'k} \times N_{i'k})})} = \frac{g_{ik}}{\sum_{i'} g_{i'k}} ,$$

where W_{ik} and N_{ik} are the total weight and the total number of prey categories i in the diet of individual k. We used GM to calculate prey category proportion in the fish's diet as a new index to compensate for prey importance in weight and number. Combining these two aspects is considered effective in depicting dietary importance of prey categories, since it allows us to take into account energy consumption (prey biomass, W_i) and foraging behaviour (prey count, N_i, see Hyslop 1980 for discussion).

VI.2.4 Habitat and prey availability

Habitat and prey availability were assessed through spatial variation in the composition of the animal demersal communities (invertebrates and vertebrates) captured during the CGFS in 2009. A hierarchical agglomerative clustering using Ward's minimum variance method with Euclidean distances adapted to binary data ("quadratic" squared Euclidean, see Legendre & Legendre 1998) was applied to species' presence-absence data. This clustering procedure allowed to identify 3 main demersal communities in the eastern English Channel (**Fig. VI.1**). Each community was characterized by 3 indicator species determined using the index of Dufrêne & Legendre (1997). This index combines values of abundance and frequency of occurrence of species in each clustering group, here communities, and the species exhibiting the three highest index values for each community were considered as indicators. Spatial location of the 3 communities was considered as reflecting habitat variation for the studied fish species since community composition reflects variation in both abiotic conditions (e.g. physico-chemical parameters) and biotic conditions (e.g. prey availability and the presence of competitors and predators). All analyses were conducted with the package "vegan" (Oksanen *et al.* 2012) of the software R.

VI.2.5 Phylogeny

To assess phylogenetic relationships between fish species, the entire DNA sequence of mitochondrial Cytochrome-*b* (1140 base pairs) was extracted from the GenBank® database for each species (Benson *et al.* 2000). Cytochrome-*b* sequence is commonly used in phylogenetic and evolutionary studies in several groups of organisms (e.g. fish, Cespedes *et al.* 1998; Dowling *et al.* 2002) and is recognized as the most useful DNA sequence to determine phylogenetic relationships between organisms (Branicki *et al.* 2003). The cytochrome-*b* sequences of all fish species were then aligned and a phylogenetic tree was computed using a maximum-likelihood algorithm (Dereeper *et al.* 2003). Finally, a matrix of phylogenetic distances between species was extracted from the phylogenetic tree and was decomposed in principal components (phyloPC), a subset of which was selected by the broken stick model (Diniz-Filho *et al.* 1998) and used as phylogenetic data in further analyses (see below).

VI.2.6 Intra-specific investigation of the determinants of trophic relationships

In order to assess the determinants of diet variation among conspecifics within each species, variance partitioning was applied to the diet matrix of each species constructed by collecting the proportion p_{ik} of each prey category i (columns) in the diet of each individual k (lines). Variance partitioning is a powerful method that combines multiple regression and canonical analyses in order to quantify the respective contributions of a set of explanatory matrices to variation in the response matrix (Borcard *et al.* 1992). This method, initially developed for continuous quantitative data based on classical Redundancy analysis (RDA), had to be adapted to compositional data such as those used for describing community composition (species-by-site matrices) or stomach contents (prey-by-individual matrices) as in our case (Peres-Neto *et al.* 2006). Variance partitioning was therefore based on multiple distance-based RDA (db-RDA, Legendre & Anderson 1999), a RDA like analysis using Bray-Curtis distance as dissimilarity index between individuals' diet since it is one of the most adapted dissimilarity index for compositional data.

For each species, this db-RDA variance partitioning was applied to the diet matrix as response matrix explained by the matrix of intraspecific morphological data, the habitat where individuals were captured, individual body size, and sex:

Individual diet ~ morphology + habitat + body size + sex

VI.2.7 Inter-specific investigation of the determinants of trophic relationships

Given that variation in body shape across species is supposed to depend on phylogeny and habitat, a first RDA with variance portioning was performed on the matrix of interspecific morphological data explained by the matrix of phylogenetic principal components (phyloPC) and habitat. This analysis was meant to quantify and remove morphological variance due to phylogeny and habitat (Desdevises *et al.* 2003) and assess the potential indirect effect of phylogeny and habitat on trophic relationships through their direct effects on morphology. The residuals of this RDA (hereafter referred to as “morphological residuals”) described variation in morphology unaccounted for by phylogeny and habitat and were used in the second analysis described below.

In a second step, the direct determinants of trophic relationships at the scale of the species assemblage were investigated. A db-RDA variance partitioning was applied to the diet matrix including all individuals of all species explained by, the matrix of phylogenetic principal components (phyloPC), the matrix of morphological residuals, the habitat where individuals were captured, and the matrix of individual state variables (body size and sex):

Individual diet ~ phylogeny + morphological residuals + habitat + individual state

Using interspecific morphological residuals in this analysis allowed us to assess the effect of morphology independent from morphological variation due to phylogeny and habitat. Individual state variables, body size and sex, had to be grouped in a single explanatory matrix as current implementations of variance portioning are limited to 4 explanatory matrices or variables. No fraction of variance could thus be attributed to body size and sex separately.

The significance of variance fractions in intra- and inter-specific db-RDA variance partitioning were assessed by permutation tests whenever possible, and adjusted R^2 were computed as an unbiased estimator of the contribution of each of these fractions to the variance explained by the model. All analyses were conducted with package “vegan” (Oksanen *et al.* 2012) of the software R.

VI.3 Results

VI.3.1 Intra-specific investigation of the determinants of trophic relationships

Across species, body size and habitat were the main factors contributing to diet variation among conspecifics, whereas morphology (intraspecific morphological data) contributed occasionally and sex did not contribute at all (**Table VI.1**). More precisely, morphology was significantly related to diet in 2 species only, plaice and mackerel, and accounted only for 1.55% and 2.69% of variance respectively. Habitat affected significantly diet in 6 species and explained a higher percentage of variance, varying between 1.34 (horse mackerel) and 8.48% (catshark) according to species (**Table VI.1**). Body size was significantly linked to diet in 11 species and generally explained an even higher fraction of variance ranging from 1.4 (seabass) to 56.26% (herring) with 7 species above 7% and 4 species above 13%. Diet was significantly affected by both body size and habitat in 4 species, namely seabass, cod, surmullet, and horse mackerel, explaining between 30.60 % and 41.09 % of variance (**Table VI.1**). In plaice, diet depended on morphology and habitat with 23.50 % of variance explained and in mackerel by morphology and size with 41.43 % of variance explained. In catshark, diet was only impacted by habitat whereas it was only affected by size in tub gurnard, sole, smoothhound, skate, herring and sprat. Finally, none of the tested factors had an effect on diet in red gurnard, whiting, and pilchard (**Table VI.1**).

Table VI.1: Results of db-RDA variance partitioning on intraspecific diets variation. Percentage of variance (adjusted R²) explained by each explanatory matrix or variable, namely morphology, body size, sex, and habitat, and by the complete model are given in corresponding columns for each species, while their significance is indicated between parentheses. *ns* = non significant, (*) P-value < 0.05, (**) *P*-value < 0.01. A Holm correction for multiple comparisons was included in P-values computation.

Species	**morpho**	**size**	**sex**	**habitat**	**% tot**
Red gurnard	*ns*	*ns*	*ns*	*ns*	58.10
Tub gurnard	*ns*	2.71 (*)	*ns*	*ns*	53.75 (*)
Seabass	*ns*	1.40 (*)	*ns*	4.08 (**)	30.60 (**)
Cod	*ns*	7.08 (**)	*ns*	3.77 (**)	40.07
Whiting	*ns*	*ns*	*ns*	*ns*	31.53
Surmullet	*ns*	2.16 (**)	*ns*	5.55 (**)	31.87 (***)
Plaice	1.55 (*)	*ns*	*ns*	3.07 (**)	23.50
Sole	*ns*	7.65 (**)	*ns*	*ns*	34.48 (*)
Smoothhound	*ns*	14.27 (**)	*ns*	*ns*	66.07 (*)
Catshark	*ns*	*ns*	*ns*	8.48 (**)	88.16
Skate	*ns*	13.19 (**)	*ns*	*ns*	69.03 (***)
Horse mackerel	*ns*	7.91 (**)	*ns*	1.34 (*)	41.09 (***)
Mackerel	2.69 (*)	3.66 (*)	*ns*	*ns*	41.43 (*)
Herring	*ns*	56.26 (**)	*ns*	*ns*	40.52 (***)
Pilchard	*ns*	*ns*	*ns*	*ns*	58.92
Sprat	*ns*	15.43 (*)	*ns*	*ns*	49.74

VI.3.2 Inter-specific investigation of the determinants of trophic relationships

The RDA applied to the matrix of interspecific morphological data detected that phylogenetic distance between species extracted from the phylogenetic tree (Fig. 3a) explained significantly 25.79% (*P*-value = 0.005) of morphological variation at the scale of the species assemblage, whereas habitat accounted for 1.51 % (*P*-value = 0.005) of variance only though significantly (**Fig. VI.3 b**). Morphological residuals extracted from this RDA, i.e. without variation due to phylogeny and habitat, were then used in the following analysis.

The db-RDA variance partitioning applied to the diet matrix including all individuals of all fish species showed that, together, phylogeny, habitat, morphological residuals, and individual state explained significantly 24.47% (*P*-value = 0.005) of individual diet variation at the scale of the assemblage. More precisely, all explanatory matrices or variables affected significantly diet (**Table VI.2**). Individual fractions of variance explained by phylogeny, habitat and individual state were very low, 3.34%, 0.90% and 0.87%, respectively, whereas morphological residuals alone explained 17.47 % of diet variation (**Fig. VI.3** and **Table VI.2**). Any combination of explanatory matrices including morphology always explained more than 20 % of variation. Without morphology, the other factors explained at best 7.90 % of variance when taken together (see **Table VI.2** for details).

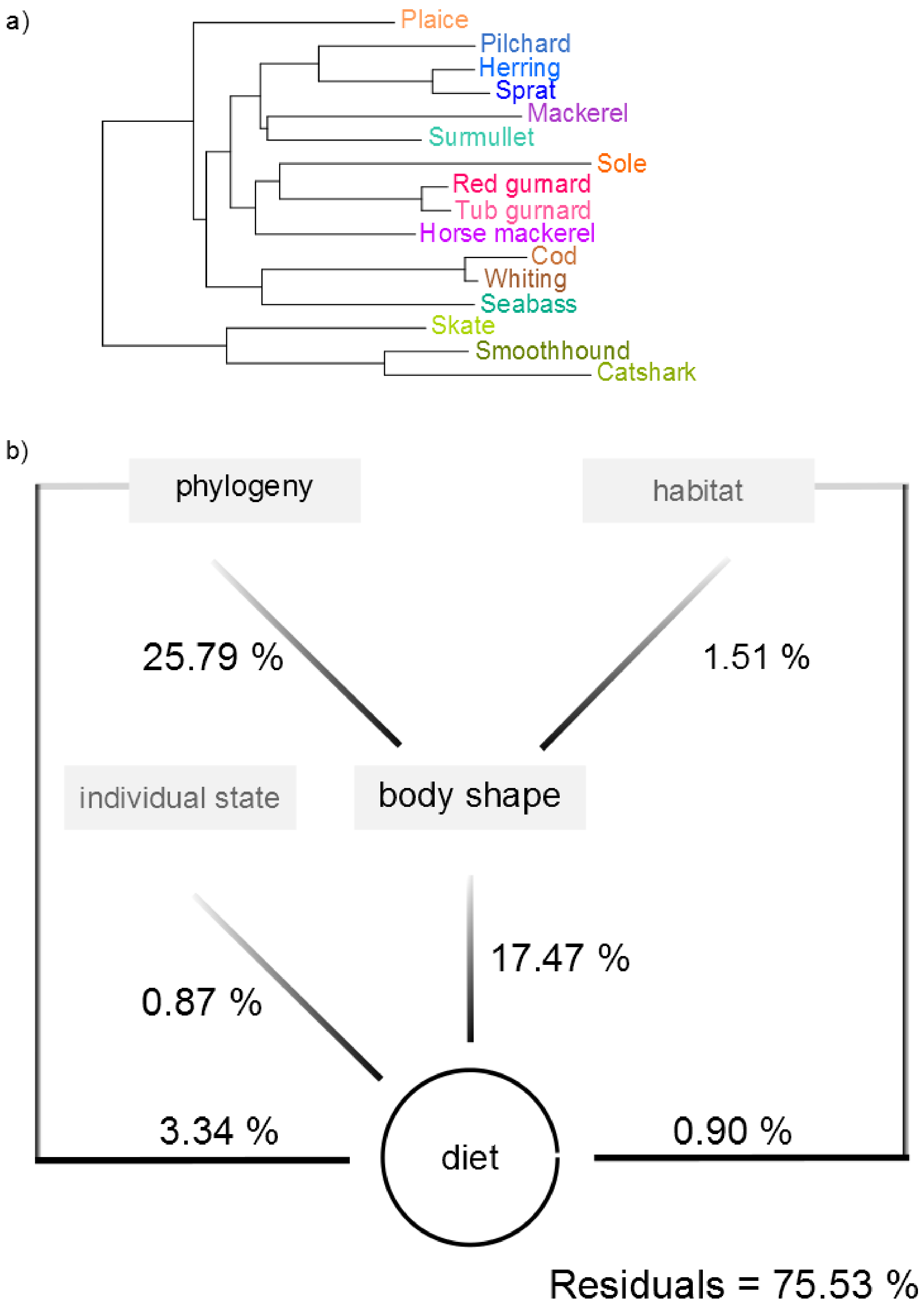

Figure VI.3: Variance partitioning scheme at the scale of the species assemblage. a) Phylogenetic tree. b) Illustration of the principal results of regarding indirect and direct effects (RDA on interspecific morphological data and db-RDA variance partitioning on diet respectively) of phylogeny, habitat and individual state on individual diet variation within the whole assemblage.

Table VI.2: Results of db-RDA variance partitioning on individual diet variation at the scale of the species assemblage. *P*-values and percentage of explained variation (adjusted R^2) are presented for each explanatory matrix (Individual variance fraction), i.e. phylogenetic Principal Components (phyloPC), habitat, individual state variables (sex and size) and morphological residuals (morphology), and each combination of explanatory matrices (Combined variance fraction).

Explanatory matrices	***P*-value**	**adjusted R^2**
Variance explained tot	**0.005**	**24.47**
Individual variance fraction		
PhyloPC	0.005	3.34
Habitat	0.005	0.90
Individual state	0.005	0.87
Morphological residuals	0.005	17.47
Combined variance fraction		
PhyloPC + Habitat	0.005	4.55
PhyloPC + Individual state	0.005	7.27
Habitat + Individual state	0.005	4.53
Morphological residuals + PhyloPC	0.005	23.49
Morphological residuals + Habitat	0.005	23.94
Morphological residuals + Individual state	0.005	21.14
PhyloPC + Habitat + Individual state	0.005	7.90
Morphological residuals + PhyloPC + Habitat	0.005	24.50
Morphological residuals + PhyloPC + Individual state	0.005	24.46
Morphological residuals + Habitat + Individual state	0.005	22.02

Our study allowed to estimate the direct and indirect effects of several factors, namely phylogeny, morphology, individual state, and habitat, on trophic relationships in a natural marine fish community and to quantify that, together, they contribute around a quarter of diet variation. Morphological variation between individuals and across species appeared to be the major factor explaining individual diet variation within the species assemblage (**Fig. VI.4**). Phylogeny had an indirect effect on diet variation, by accounting for an important part of morphological variation, but its direct effect was minor (**Fig. VI.4**). At the assemblage scale, habitat and individual state variable had weak effects on individual diet variation, whereas at intra-specific level, they accounted for a substantial amount of diet variation among conspecifics for a majority of species. In this study, 75 % of variation in trophic relationships remained unexplained (**Fig. VI.4**).

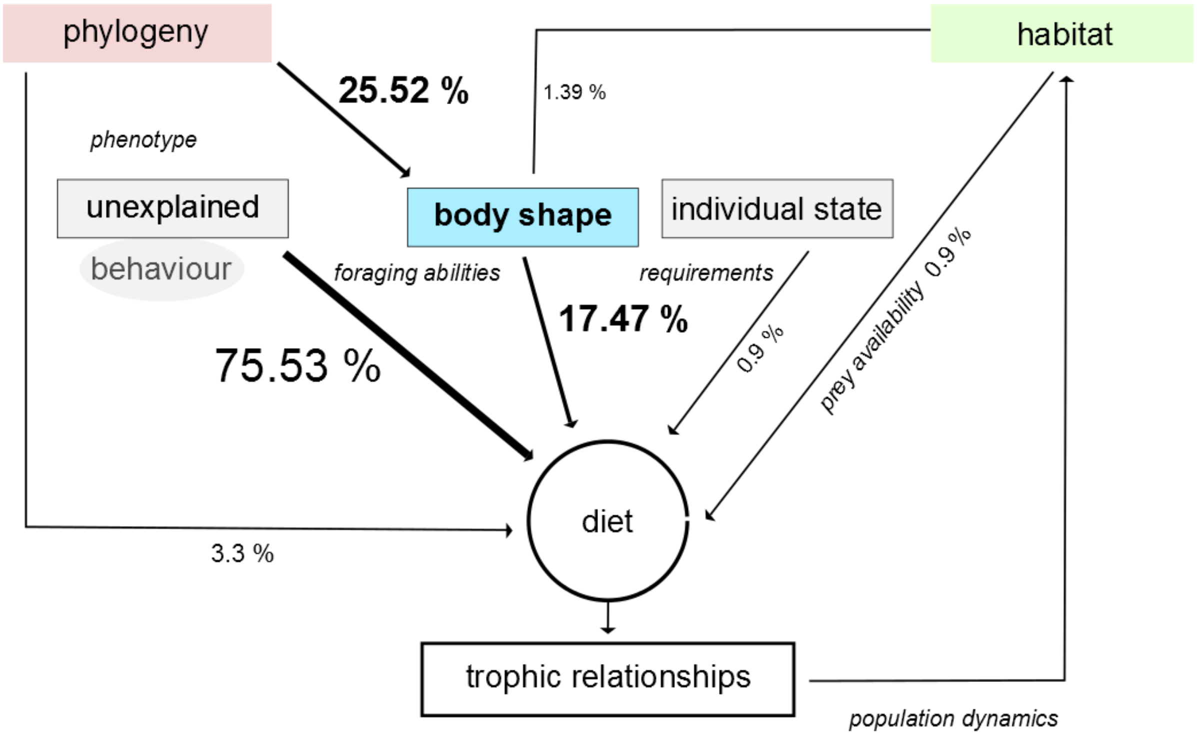

Figure VI.4: Diagram of potential causes and consequences of trophic relationships. The direct and indirect contributions of several factors to variation estimated in this paper are summarized.

VI.4.1 From diet variation between conspecifics…

One of our aims was to identify factors explaining diet variation among conspecifics. We initially expected prey availability to play an important role in individual diet determinism, since an individual will only consume prey it encounters (Ferry-Graham *et al.* 2002). Habitat, defined by the spatial location of different animal communities and thus used as an indicator of available prey diversity, appeared indeed as one of the significant factors that explained individual diet variation within a number of species. However, it had a moderate influence only, which was surprising since we detected a certain degree of heterogeneity at mesoscale (i.e. at the scale of the eastern English Channel area) in the community composition and thus expected contrasted diets between conspecifics caught in different habitats. This surprising lack of forthright effect may, however, results from the ability of the studied fish species to move easily across habitats at mesoscale and thus to find their preferred prey items, exhibiting a certain degree of food selectivity (feeding preferences). In other words, habitat variation will result in diet variation across conspecifics if its spatial scale is larger than that of individuals' foraging area. This result also suggests that the studied fish species are not opportunistic feeders, since opportunism combined with spatial heterogeneity in prey availability would have generated an important effect of habitat on diet. Opportunism occurs when a predator attacks a non-preferred prey species without prior intention (Cressman & Garay 2010) and is different from versatility, which is the ability to attack a wide diversity of prey depending on environmental conditions, be they biotic or abiotic.

The main factor affecting intraspecific diet variation was individual body size as we found a size effect for a majority of species (11 out 16) that contributed for a moderate to substantial fraction of variation (>7%) for 7 of them. It is worth noticing, however, that two species, sprat and herring, for which the fraction of explained variation was high (15.43% and 56.26%, respectively) are highly specialized (planktivorous) and thus that individuals generally differ very little in terms of diet. Digestive tracts contents indeed confirmed that absolute variation in diet between conspecific is weak and related to a few prey items only, so that even small differences in diet due to size may explain a large proportion of variation. Nevertheless, the generalized influence of body size on intra-specific diet variation found in this study tend to support the common idea that size is a proxy for trophic position (Brown & Gillooly 2003; Trebilco *et al.* 2013) and influences trophic relationships even within species, notably because of ontogenic changes in diet (Scharf *et al.* 2000), however the correlation between body size and diet was, however, not perfect as except for herring, the explained variance was less than

16%. Several empirical studies (Price 1987; Ingram *et al.* 2011) already showed that, contrary to the assumption of numerous theoretical studies, size cannot perfectly predict diet and suggested that other morphological traits could better explain diet variation. In this study, we decided to investigate the influence of the whole body shape on intraspecific variation in diet but detected a significant weak effect for 2 species only, plaice and mackerel. This result is in opposition with the expectation that variation in body shape would imply foraging differences between conspecific (Svanbäck & Eklöv 2003). It may be possible that body shape is not the most relevant morphological characteristic for diet determinism and that we should rather focus on trophic morphological traits, such as mouth gape or gill rakers. However, most trophic morphological traits are varying weakly among conspecifics because of strong canalization (e.g. the number of gill rakers or teeth are highly genetically coded) and thus are not relevant for an intra-specific approach.

Sex dimorphism in terms of behaviour or physiological requirements is also expected to induce difference in diet between conspecifics (Araùjo *et al.* 2011), but gender did not affect diet in any of the studied species. This may be related to the fact that sexual dimorphism in fish is very often expressed in terms of body size or body shape (e.g. Rijnsdorp & Ibelings 1989; Saillant *et al.* 2001; Bromley 2003) and that these factors were already included our analysis.

Even when diet was affected by some of the factors tested, a large part of its variation between conspecifics remained unexplained. According to Optimal Foraging Theory differences in diet between conspecifics should be mainly attributable to differences in prey availability and abundance, feeding phenotypes, physiological requirements and/or feeding behaviour (Svanbäck & Bolnick 2008). Since prey availability and abundance reflected here in habitat, and feeding phenotypes and physiological requirements, depicted here by body size, body shape, and sex, were included in our analysis, individual feeding behaviour appears as a logical candidate for explaining this large part of intra-specific diet variation. Behaviour is probably the most plastic trait in organisms, and is much more labile than morphology (West-Eberhard 1989). Differences in feeding behaviour between conspecific, i.e. animal personality, were already described in several taxa and pointed out as the main explanation for differences in individual diet (Estes *et al.* 2003; Sih *et al.* 2004; Woo *et al.* 2008; Wolf & Weissing 2012). We should stress here that we do not deny the influence of other factors mentioned above, some of which were tested in our study, but that we hypothesise that a large part of the variation in diet between conspecifics is probably attributable to variation in feeding behaviour.

VI.4.2 …to variation in trophic relationships in the community

The principal objective of this paper was to identify the main determinants of trophic relationships at the level of the species assemblage. Although habitat, individual state and phylogeny had a significant effect, morphology was clearly the main direct factor affecting individual diet in the assemblage as it explained almost 18 % of variation alone.

The direct effect of morphology on trophic interactions was found after removing 25% of morphological variation due to phylogeny. It results that the 3.3% of individual diet variation within the assemblage explained by phylogeny should include the direct effect of phylogeny on feeding behaviour and its indirect effect through morphology (phylogeny and morphological residuals used in the analysis were orthogonal factors). Phylogeny has therefore a very moderate influence on trophic relationships in the assemblage, be it direct or indirect, which suggests that phylogenetic diversity alone is not a good predictor of trophic diversity. More generally, these results suggest that phylogeny should not be used as a surrogate for functions performed by organisms, among which energy and biomass transfer through trophic relationships, and that taxonomic diversity is probably not a good proxy for functional diversity (Ferry-Graham *et al.* 2002; Naeem & Wright 2003; Price *et al.* 2011; Best *et al.* 2013).

The fact that morphology was the main factor explaining individual diet variation in the assemblage was consistent with the idea that the ability of a predator to forage on a prey is partly constrained by its body shape, which in turn influences its swimming (movement and speed), hunting, and handling ability (Motta *et al.* 1995; Wainwright & Richard 1995; Ferry-Graham *et al.* 2002). The important proportion of diet variation in the assemblage accounted for by morphology is in accordance with other studies on fish (Mediterranean sea Albouy *et al.* 2011, coral reef Bellwood *et al.* 2006, freshwater streams Douglas & Matthews 1992; Ibanez *et al.* 2007, and lake Svanbäck & Eklöv 2003). Despites the fact that our study supports the idea that morphology partly shapes trophic relationships in natural community, 75 % of diet variation within the assemblage remained unexplained and unpredictable (Albouy *et al.* 2011).

The link between morphology and diet is somewhat controversial in fish. Some authors found no (or non-significant) correlation between morphology and diet (or trophic characteristics) in fish species (Douglas & Matthews 1992; Labropoulou & Markakis 1998; Bolnick & Paull 2009). Such mismatch between morphology and diet was even at the origin of the so-called “Liem’s paradox” (Liem 1980) according which many apparently specialized fish species may act like trophic generalists. In contrast, other authors found a relatively weak but significant relationships between fish morphology and diet (Wainwright & Richard 1995; Wainwright & Bellwood 2002; Svanbäck & Eklöv 2003; Ibanez *et al.* 2007). The common result between all these studies, however, was a large and unpredictable variation in fish diet as in our case. In order to explain the absence of/or the weak relationship between morphology and diet and the resulting large unpredictability of diet variation in fish species, many authors agreed on invoking the importance of feeding versatility in fish (Robinson & Wilson 1998; Bellwood *et al*. 2006; Albouy *et al*. 2011). Feeding versatility is based on the idea, first, that different morphologies can exploit common prey items that do not require particular morphological attributes and, second, that foraging behaviour is particularly versatile in fish and independent from their morphology to the extent that morphology may not predict precisely fish feeding habits (Liem 1980; Liem & Summers 2000; Binning *et al.* 2009). Our study supports the versatility hypothesis and showed that, even if morphology is an important factor influencing individual diet variation across species, it is highly probable that feeding behaviour is the major factor implicated in trophic relationships in a community.

Behavioural differences between conspecifics and species are common in animal species and have many implications. Evolutionarily, behavioural versatility is critical for fitness because it is directly implicated in feeding strategy and thus energy intake, but also in predator avoidance, mating strategy, and/or social interactions (Wolf & Weissing 2012). Ecologically speaking, versatility allows species to respond to changes in biotic and abiotic conditions, affects directly intra- and inter-specific interactions such as competition and predation, and plays a role in indirect species interactions (trait-mediated indirect interactions TMII, Griffen *et al.* 2012). TMII are indirect biotic interactions, i.e. the effects of a species on a second species via its interactions with a third one (interactions between multiple predators sharing the same prey for example) that depend on organism’s trait, notably behaviour, physiology or morphology. TMII are thus of major importance for the structure of natural communities (Griffen *et al.* 2012). To conclusion, behavioural versatility impacts structure and dynamics of population and ecological networks, supports biodiversity by relaxing trophic competition (whether it is intra- or inter-specific) and promotes species coexistence (Ferry-Graham *et al*. 2002; Bellwood et al. 2006; Wolf & Weissing 2012). It is therefore fundamental to assess the implication of feeding versatility for trophic relationships in natural communities by, for instance, developing experimental studies aiming at the behavioural component of feeding strategy.

VI.4.3 Concluding remarks

This study showed that despite its effect on body shape, phylogeny has a weak effect on trophic relationships, whereas morphological variation in body shape independent from phylogeny is one of the main determinants of individual diet. Besides trophic interactions, body shape may be implicated in several ecological functions performed by organisms and it is probable that morphological diversity may be related to other ecosystem processes (Ricklefs 2012). Behaviour may be involved in the large part of unexplained variation in individual diet despite morphological determinism. Individual personality is now known to have implications for community structure (Post *et al.* 2008; Bolnick *et al.* 2011). Particularly, personality may be a major determinant of trophic relationships, specifically in fish species that exhibit a high degree of feeding versatility (Albouy *et al.* 2011). Since trophic relationships underlie a keystone ecological process, i.e. the transfer of energy and biomass, behaviour is thus likely to have important implications for ecosystem functioning.

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Annexes

Josette Cachera

ANNEXE 1: Results of the hierarchical clustering on presence/absence data characterizing communities of the survey using the Dufrêne-Legendre species indicator value.

Species	**Community**	**Indicator value**
Pleuronectes platessa	1	0,76
Limanda limanda	1	0,68
Merlangius merlangus	1	0,67
Callionymus lyra	1	0,43
Solea vulgaris	1	0,42
Trigla lucerna	1	0,42
Liocarcinus holsatus	1	0,42
Trachinus vipera	1	0,36
Dicentrarchus labrax	1	0,33
Macropipus puber	1	0,33
Alcyonidium diaphanum	1	0,32
Clupea harengus	1	0,31
Platichthys flesus	1	0,31
Buglossidium luteum	1	0,30
Trisopterus luscus	1	0,29
Gobiidae	1	0,29
Sepiola	1	0,25
Sprattus sprattus	1	0,25
Agonus cataphractus	1	0,24
Crangon crangon	1	0,22
Alcyonium digitatum	2	0,51
Sepia officinalis	2	0,47
Mullus surmuletus	2	0,42
Aequipecten opercularis	2	0,40
Aspitrigla cuculus	2	0,40
Loligo forbesi	3	0,51
Spondyliosoma cantharus	3	0,43
Scyliorhinus caniculus	3	0,41
Mustelus asterias	3	0,35
Crossaster papposus	3	0,33
Scyliorhinus stellaris	3	0,30
Porifera	3	0,28

ANNEXE 2: Anatomical descriptions of (semi-)landmarks' localisation

points number	**anatomic correspondence**
1	anterior end
2	eye vertical
3	posterior end of head
4	1st dorsal quarter of standard length
5	dorsal standard length centre
6	3rd dorsal quarter of standard length
7	dorso-anterior of caudal peduncle
8	dorso-posterior of caudal peduncle
9	dorsal tail
10	middle of tail
11	ventral tail
12	ventro-posterior of caudal peduncle
13	ventro-anterior of cauldal peduncle
14	3rd ventral quarter of standard length
15	ventral standard length centre
16	1st ventral quarter of standard length
17	ventral opercule
18	chin angle
19	posterior end of caudal peduncle
20	top of jaw
21	1st angle of opercule
22	2nd angle of opercule

ANNEXE 3: Complete description of prey categories and sources for the calculation of prey categories' trophic levels.

Prey categories	Identified prey	Species used as equivalent	TL	Source	Mean TL
Others					2.62
	Algae		1.00	(Grall, *et al.*, 2006)	
	Insect				
	Cirolanidae				
	Gnathiidae		3.90	(Fanelli, et al., 2009)	
	Isopod				
	Rissoides desmaresti	*Squilla mantis*	2.60	www.seaaroundus.org	
	Sponge				
	Balanus sp		3.00	(Jiming 1982)	
Amphipod					2.60
	Ampeliscidae				
	Amphilochidae				
	Amphipod	*Gammarus wilkitzkii*	2.60	(Hobson & Welch 1992)	
	Atylidae				
	Calliopidae				
	Leucothoidae				
	Pontoporeiidae				
	Stenothoidae				
Large bivalve					2.25
	Azorinus chamasolen				
	Bivalvia				
	Crassostrea sp				
	Mytilus edulis		2.00	www.seaaroundus.org	
	Chlamys varia		2.50	(Grall *et al.*, 2006)	
	Mactridae				
Carnivorous Polychaete					2.73
	Aphrodita aculeata				
	Flabelligeridae		2.30	(Jiming 1982)	
	Eunicidae	*Eunice harasii*	3.50	(Grall *et al.*, 2006)	

	Glycera sp				
	Glyceridae				
	Nephthyidae				
	Nereidae		2.40	(Jiming 1982)	
Un. cephalopod					3.50
	Unidentified cephalopod		3.50		
Clam					2.05
	Abra alba				
	Arca tetragona				
	Abra sp				
	Cardiidae				
	Donax vittatus		2.00	www.seaaroundus.org	
	Laevicardium crassum				
	Gari sp				
	Mactra glauca	*Mactra sachalinensis*	2.10	www.seaaroundus.org	
	Nucula hanleyi				
	Nucula nitidosa				
	Nucula sp				
	Veneroida				
Pelagic fish					4.08
	Aloa alosa				
	Clupea harengus		3.80	(Jennings *et al.* 2002)	
	Clupeidae				
	Sardina pilchardus		3.10	www.seaaroundus.org	
	Sprattus sprattus		4.30	(Jennings *et al.* 2002)	
	Trachurus trachurus		5.10	(Jennings *et al.* 2002)	
	Scomber scombrus				
Copepod					2.20
	Calanus elongatus	*Calanus finmarchicus*	2.30	(Jiming 1982)	
	Copepod	*Pseudocalanus sp*	2.10	(Jiming 1982)	
	Harpacticoida				
Walking crab					3.13

	Atelecyclidae				
	Brachyura				
	Corystes cassivelaunus				
	Carcinus maenas		3.50	www.seaaroundus.org	
	Cancer pagurus		2.60	www.seaaroundus.org	
	Ebalia cranchii				
	Ebalia tuberosa				
	Ebalia sp				
	Goneplax rhomboides				
	Necora puber		2.60	www.seaaroundus.org	
	Pilumnus hirtellus		3.80	(Grall *et al.* 2006)	
	Pinnotheres pisum				
	Portunidae				
	Rhithropanopeus harrisii				
	Thia scutellata				
	Xanthidae				
Other decapod					3.00
	Anomoura				
	Crustacean				
	Decapod		3.00		
Crustacean larvae					2.25
	Crustacean larvae		2.00		
	Megalopoda		2.50	(Jiming 1982)	
	Praniza				
	Zoa				
Cumacea					2.30
	Bodotria arenosa				
	Bodotria scorpionides				
	Bodotria sp				
	Bodotriidae			(Fanelli *et al.* 2009)	
	Cumacea		2.60 &2.00		
	Nebalia bipes				
	Nebalia sp				

	Pseudocuma sp				
	Pseudocumatidae				
	Vaunthompsonia sp				
Cuttlefish					3.55
	Rossia macrosoma				
	Sepiola atlantica				
	Sepia elegans				
	Sepiolidae	*Sepia officinalis*	3.55	www.seaaroundus.org	
Dragonet					3.80
	Callionymus lyra		3.30	(Froese & Pauly 2013)	
	Callionymus maculatus		3.30	(Froese & Pauly 2013)	
	Callionymus reticulatus				
	Callionymus sp		4.80	(Jennings *et al.* 2002)	
Echinoderm					2.30
	Echinoderm	*Thyone fusus*	2.30	(Grall *et al.* 2006)	
	Astropecten sp			www.seaaroundus.org	
Other fish					3.43
	Anguilla anguilla				
	Pholis gunellus				
	Teleost				
	Trigla sp		3.51	www.seaaroundus.org	
	Cottidae				
	Mullus surmuletus		3.35	www.seaaroundus.org	
Flat fish					4.70
	Arnoglossus imperialis				
	Pleuronectidae	*Pleuronectes platessa*	4.40	(Jennings *et al.* 2002)	
	Pleuronectiform				
	Solea solea		5.00	(Jennings *et al.* 2002)	
Gadidae					4.21
	Gadidae				
	Trisopterus luscus		3.73	www.seaaroundus.org	
	Trisopterus minutus		3.60	www.seaaroundus.org	

	Merlangius merlangus		5.30	(Jennings *et al.* 2002)	
Gastropod					2.80
	Crepidula fornicata		2.60	(Grall *et al.* 2006)	
	Gastropod		3.00 (busicon)	www.seaaroundus.org	
	Hinia sp				
	Rissoella diaphana				
	Trivia sp				
Gobie					3.11
	Gobiidae		3.11	www.seaaroundus.org	
Hermit crab					2.60
	Pagurus bernhardus				
	Paguridae				
	Pagurus sp		2.60	(Jiming 1982)	
Indeterm	Indeterm		2.00		2.00
Majidae					3.30
	Inachus dorsettentis				
	Inachus sp				
	Macropodia rostrata				
	Macropodia tenuirostris				
	Macropodia sp				
	Majidae	*Hyas sp*	3.30	(Jiming 1982)	
Other mollusc					3.00
	Opistobranchia				
	Scaphopod				
	Mollusc		3.00		
Mysid					2.40
	mysid		2.40	(Jiming 1982)	
Ophiuroid					3.00
	Amphiura sp				
	Amphiuridae				
	Ophiothrix fragilis		3.00	(Jiming 1982)	

	Ophiura ophiura		3	(Jiming 1982)	
	Ophiura sp				
	Ophiuridae				
	Ophiothrix sp				
Pelagic shrimp					2.00
	Pasiphaea sp		2.00		
Plankton					2.00
	Tanaidacea		2.00	(Fanelli *et al.* 2009)	
	Ostracod				
Other polychaete					2.30
	Arenicolidae				
	Lanice conchilega				
	Maldanidae				
	Opheliidae				
	Pectinaria koreni				
	Pectinaria sp				
	Pectinariidae		2.30	(Jiming 1982)	
	Phyllodocida				
	Polychaeta				
	Spionidae				
	Syllidae				
	Terebellidae		2.30	(Jiming 1982)	
Porcelain crab					2.50
	Pisidia longicornis		2.50	(Grall *et al.* 2006)	
	Porcellana platycheles				
	Pisidia sp				
	Porcellana sp				
	Porcellenidae				
Razor					2.05
	Ensis sp		2.00	www.seaaroundus.org	
	Phaxas pellucidus				
	Solenidae	*Ensis ensis*	2.10	www.seaaroundus.org	

Sandlance					3.11
	Ammodytes sp		3.11	www.seaaroundus.org	
	Ammodytidae				
	Hyperoplus lanceolatus				
	Hyperoplus sp				
Seasnail					2.80
	Buccinidae	*buccinum undatum*	3.60	(Grall *et al.* 2006)	
	Calliostoma sp				
	Hydrobia ulvae				
	Littorina neritoides				
	Lacuna sp				
	Lacunidae				
	Littorina sp		2.00	www.seaaroundus.org	
	Littorinidae				
	Nassaridae				
	Naticidae				
	Policines sp				
	Rissoidae				
	Skeneidae				
	Trophonopsis muricanus				
	Trochidae				
	Turbinidae				
Sessile cnidaria					2.70
	Actinaria sp				
	Anemona	*Anemona viridis*	2.70	(Grall *et al.* 2006)	
	Campanulariidae				
	Eudendrium sp				
	Hydrozoa				
	Sertulariidae				
Shrimp					2.92
	Crangon crangon		3.19	www.seaaroundus.org	
	Carida				

	Crangon sp		3.20	(Jiming 1982)	
	Crangonidae				
	Eualus gaimardii				
	Eualus occultus				
	Hyppolyte varians				
	Hippolytidae				
	Pandalina brevirostris				
	Processa canaliculata				
	Processa edulis				
	Philocheras fasciatus				
	Pandalus montagui		2.30	www.seaaroundus.org	
	Philocheras sculptus				
	Palaemon serratus				
	Philocheras trispinosus				
	Palaemon sp	*Palaemon serratus*	2.70	www.seaaroundus.org	
	Pandalidae				
	Pandalina sp				
	Pandalus sp		3.20	(Jiming 1982)	
	Philocheras sp				
	Processa sp				
	Processidae				
Sipuncle					3.10
	Sipuncle				
	Golfingia sp		3.10	(Grall *et al.* 2006)	
Squat lobster					3.10
	Galathea dispersa				
	Galathea intermedia				
	Galathea squamifera				
	Galathea strigosa				
	Galathea sp				
	Galatheidae		3.10	www.seaaroundus.org	
	Munida rugosa				
Squid					4.18

	Alloteuthis sp				
	Illex coindetii		4.15	www.seaaroundus.org	
	Loligo forbesii		4.29	www.seaaroundus.org	
	Loligo vulgaris		4.10	www.seaaroundus.org	
	Loliginidae				
	Ommastreophidae				
Swimming crab					3.15
	Liocarcinus depurator		2.60	www.seaaroundus.org	
	Liocarcinus holsatus				
	Liocarcinus marmoreus				
	Liocarcinus pusillus		3.70	(Grall *et al.* 2006)	
	Liocarcinus sp				
Thalassinidae					2.39
	Axiidae				
	Callianassa tyrrhena				
	Callianassa sp		2.20	www.seaaroundus.org	
	Callianassidae				
	Upogebia deltaura				
	Upogebia stellata				
	Upogebia sp				
	Upogebiidae	*Upogebia pugettensis*	2.57	www.seaaroundus.org	
Urchin					2.41
	Clypeasteroida				
	Echinocyamus pusillus				
	Echinoidae	*Echinus esculentus*	2.30 & 2.51	www.seaaroundus.org	
	Echinocardium sp				
	Loveniidae				
	Parvicardium sp				
	Spatangoida				

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ANNEXE 4: Description of fish species.

(note: cumulative prey curve is a technique assessing sample size sufficiency, cf Ferry, L.A. & Cailliet, G.M. (1996). Sample size and data analysis: are we characterizing and comparing diet properly? Presented at the Gutshop '96: Feeding ecology and nutrition in fish, American Fisheries Society, San Francisco, pp. 71–80.)

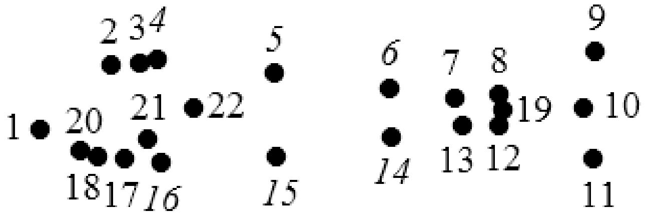
Framework of prey categories

prey type	prey category	color
cephalopod	cephalopod	seagreen
cephalopod	cuttlefish	seagreen
cephalopod	squid	seagreen
polychaete	carnivorous_polychaeta	grey
polychaete	polychaeta	grey
other prey	indeterm	black
other prey	others	black
other prey	sessile_cnidaria	black
other prey	sipuncle	black
teleost	dragonets	blue
teleost	fish	blue
teleost	flat_fish	blue
teleost	gadidae	blue
teleost	gobie	blue
teleost	pelagic_fish	blue
teleost	sandlance	blue
mollusc	clam	purple
mollusc	gastropod	purple
mollusc	large_bivalvia	purple
mollusc	mollusc	purple
mollusc	razor	purple
mollusc	seasnail	purple
crustacean	crab	orange
crustacean	crustacean	orange
crustacean	hermit_crab	orange
crustacean	majidae	orange
crustacean	pelagic_shrimp	orange
crustacean	porcelain_crab	orange
crustacean	shrimp	orange
crustacean	squat_lobster	orange
crustacean	swimming_crab	orange
crustacean	thalassinidea	orange
plankton	amphipod	green
plankton	copepod	green
plankton	crustacean_larvae	green
plankton	cumacea	green
plankton	mysid	green
plankton	plankton	green
echinoderm	echinoderm	yellow
echinoderm	ophiuroid	yellow
echinoderm	urchin	yellow

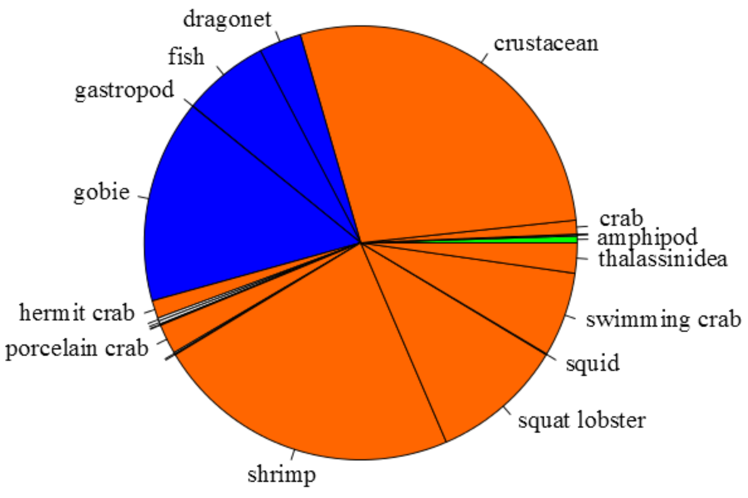
Chelidonichthys cuculus (Linnaeus, 1758)   Actinopterygii, Scorpaeniformes, Triglidae

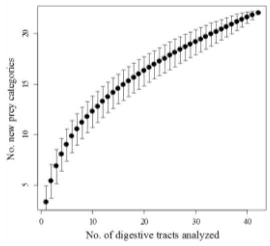
Grondin rouge / Red gurnard

Forme moyenne / mean shape



Régime alimentaire / diet   Courbe cumulée des proies / Cumulative prey curve



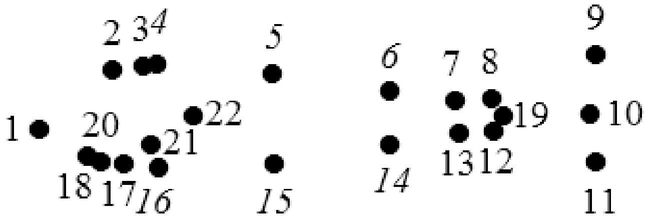


cephalopod
clam
indeterm
large bivalvia
mysid
polychaeta
sea snail
sessile cnidaria

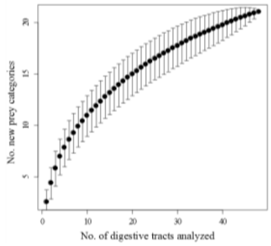
Chelidonichthys lucerna (Linnaeus, 1758) Actinopterygii, Scorpaeniformes, Triglidae

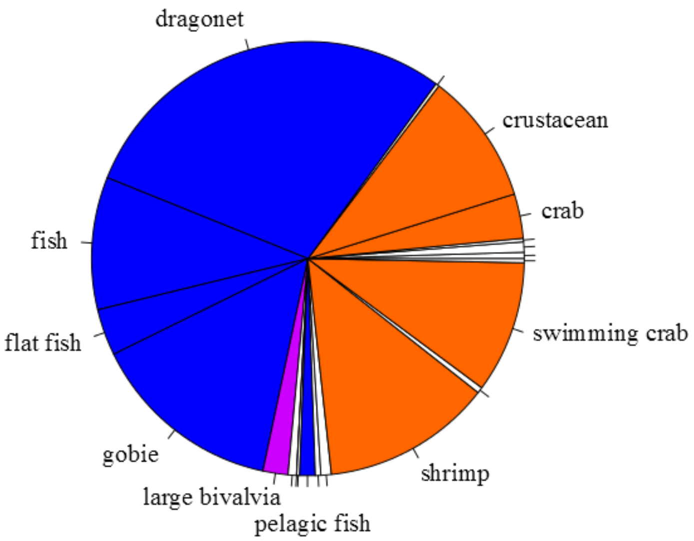
Grondin perlon / Tub gurnard

Forme moyenne / mean shape



Régime alimentaire / diet Courbe cumulée des proies / Cumulative prey curve

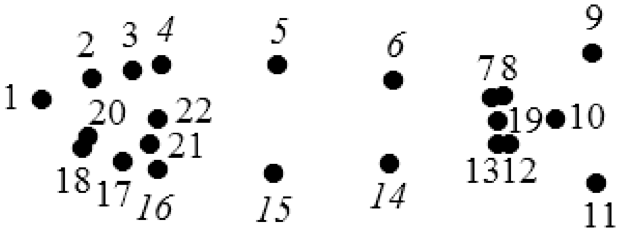




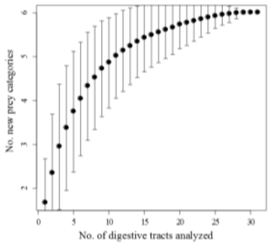
Clupea harengus (Linnaeus, 1758) Actinopterygii, Clupeiformes, Clupeidae

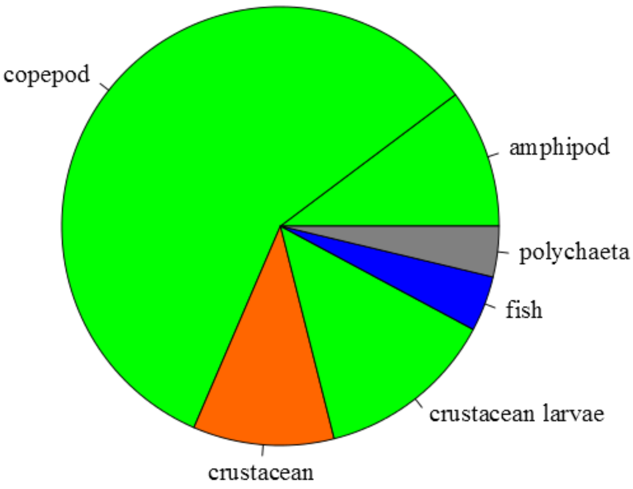
Hareng / Atlantic herring

Forme moyenne / mean shape



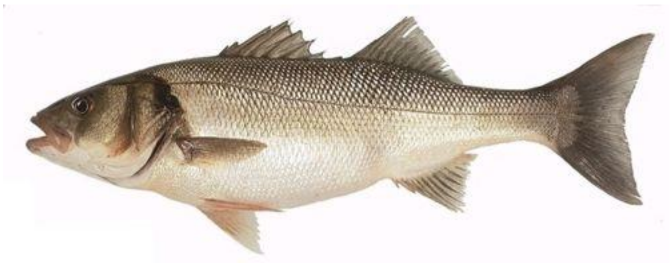
Régime alimentaire / diet Courbe cumulée des proies / Cumulative prey curve



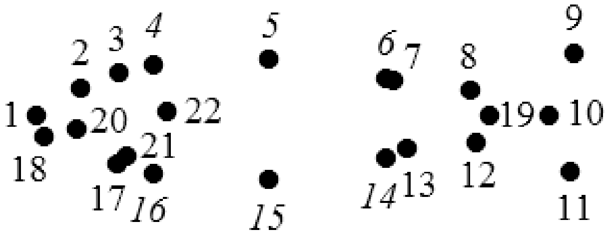


Dicentrarchus labrax (Linnaeus, 1758) Actinopterygii, Perciformes, Moronidae

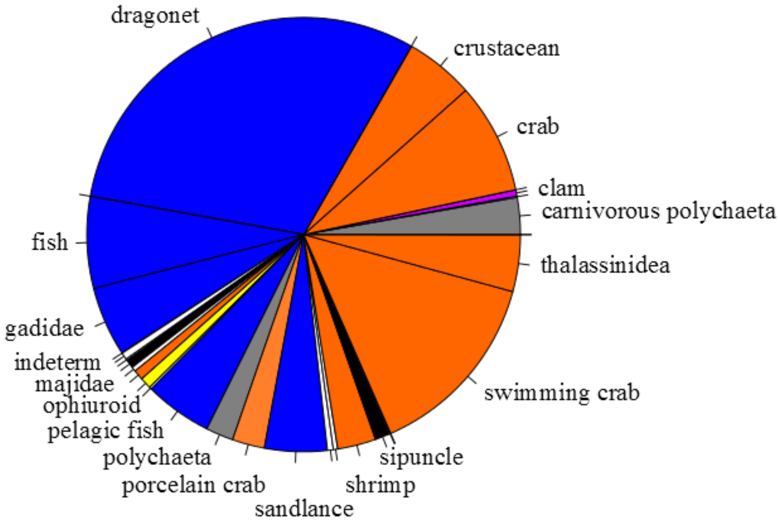
Bar commun / European seabass

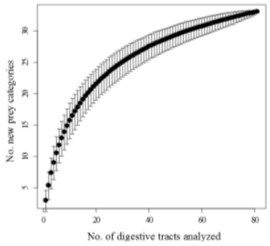


Forme moyenne / mean shape



Régime alimentaire / diet Courbe cumulée des proies / Cumulative prey curve



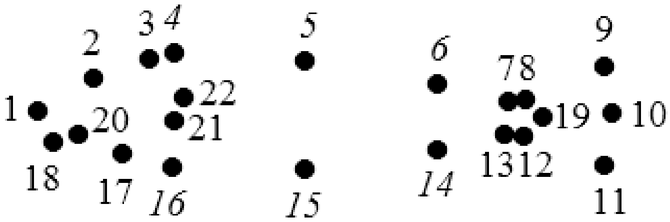


amphipod
cephalopod
copepod
crustacean larvae
echinoderm
gastropod
gobie
hermit crab
large bivalvia
others
seasnail
sessile cnidaria
squat lobster
squid
urchin

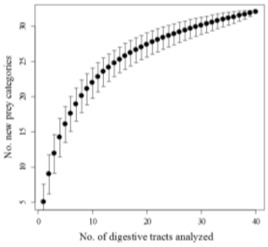
Gadus morhua (Linnaeus, 1758) Actinopterygii, Gadiformes, Gadidae

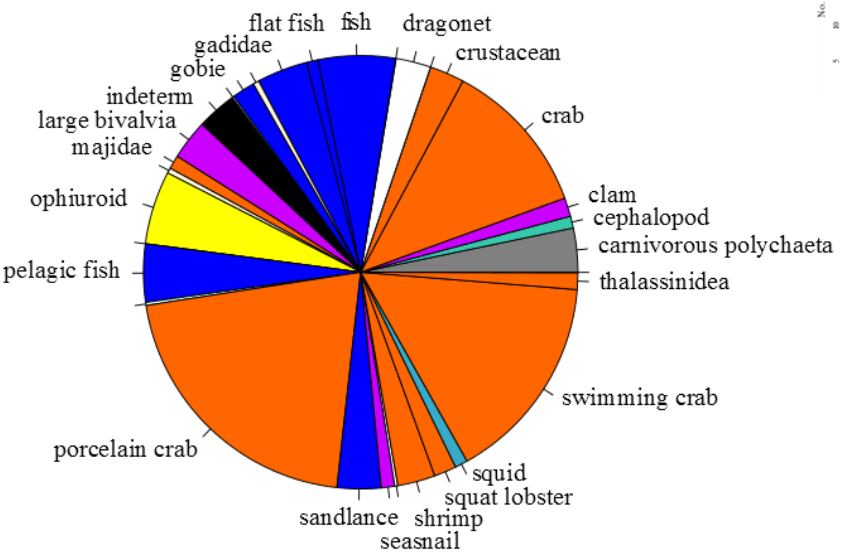
Morue / Atlantic cod

Forme moyenne / mean shape



Régime alimentaire / diet Courbe cumulée des proies / Cumulative prey curve

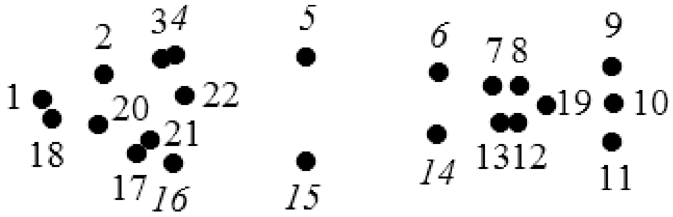




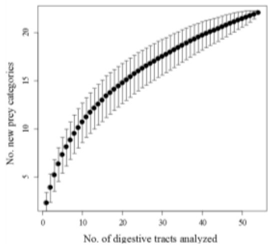
Merlangius merlangus (Linnaeus, 1758)   Actinopterygii, Gadiformes, Gadidae

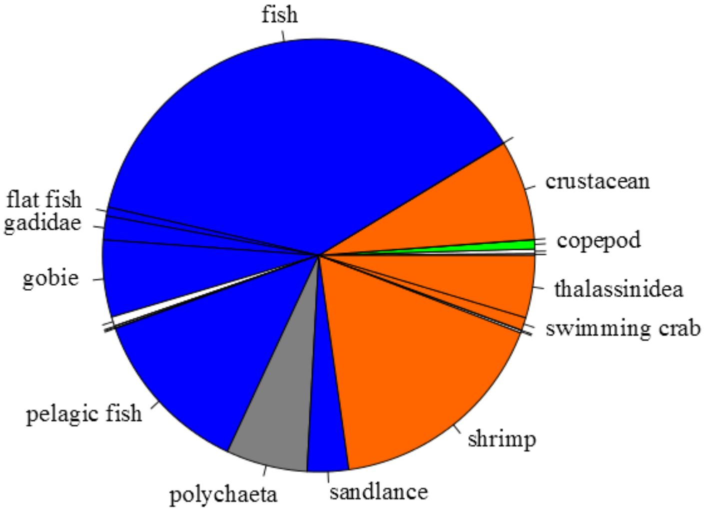
Merlan / Whiting

Forme moyenne / mean shape



Régime alimentaire / diet   Courbe cumulée des proies / Cumulative prey curve



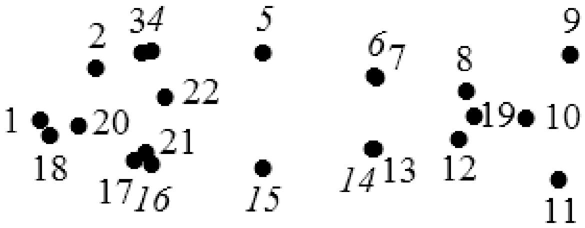


amphipod
cephalopod
crab
cuttlefish
indeterm
large bivalvia
majidae
mysid
squat lobster
squid

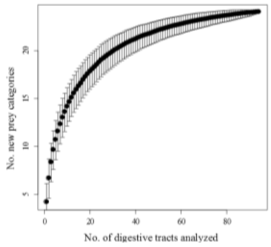
Mullus surmuletus (Linnaeus, 1758) Actinopterygii, Perciformes, Mullidae

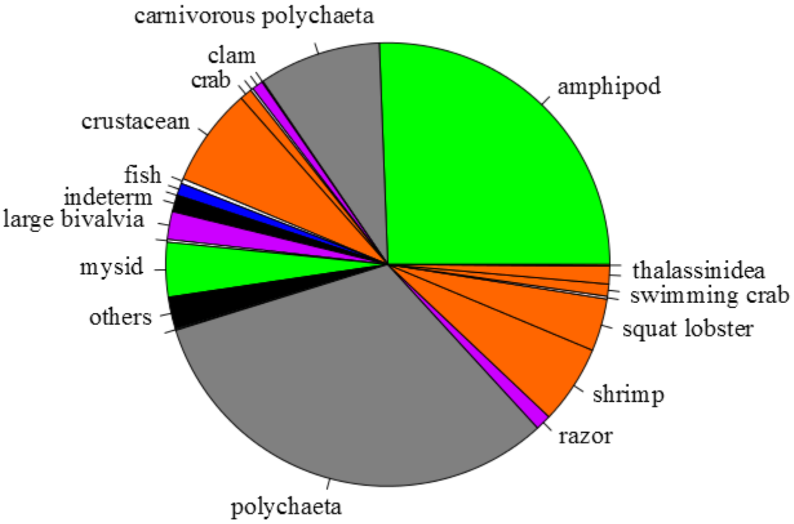
Rouget barbet / Surmullet

Forme moyenne / mean shape



Régime alimentaire / diet Courbe cumulée des proies / Cumulative prey curve



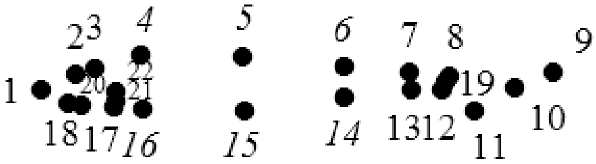


crustacean larvae
cephalopod
copepod
cumacea
majidae
plankton
squid
urchin

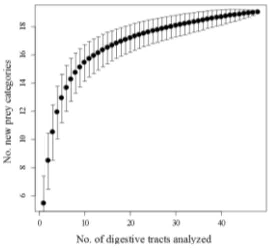
Mustelus asterias (Cloquet, 1819) Elasmobranchii, Carcharhiniformes, Triakidae

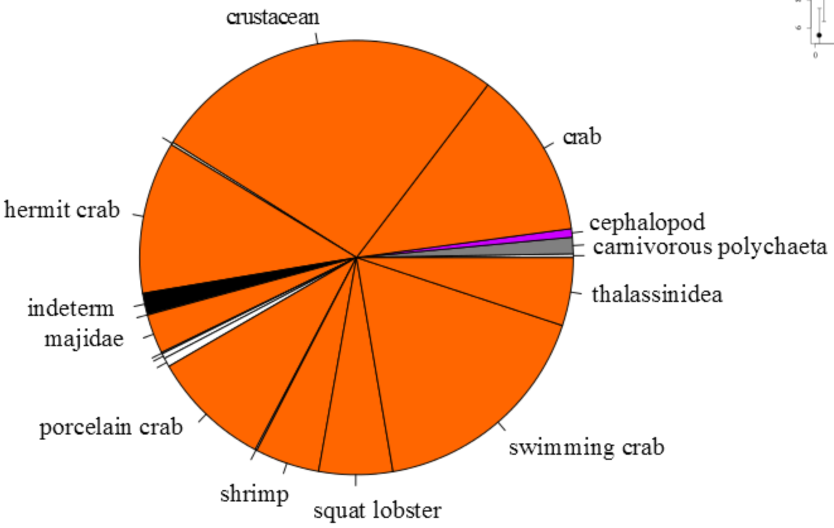
Emissole tachetée / Starry smoothhound

Forme moyenne / mean shape



Régime alimentaire / diet Courbe cumulée des proies / Cumulative prey curve

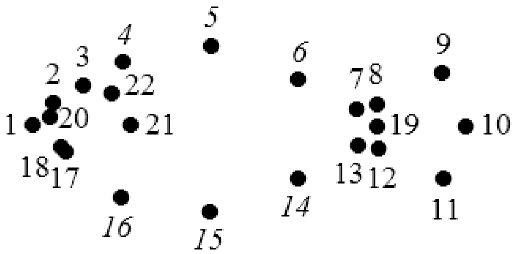




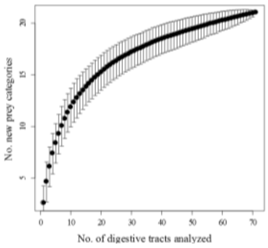
Pleuronectes platessa (Linnaeus, 1758)   Actinopterygii, Pleuronectiformes, Pleuronectidae

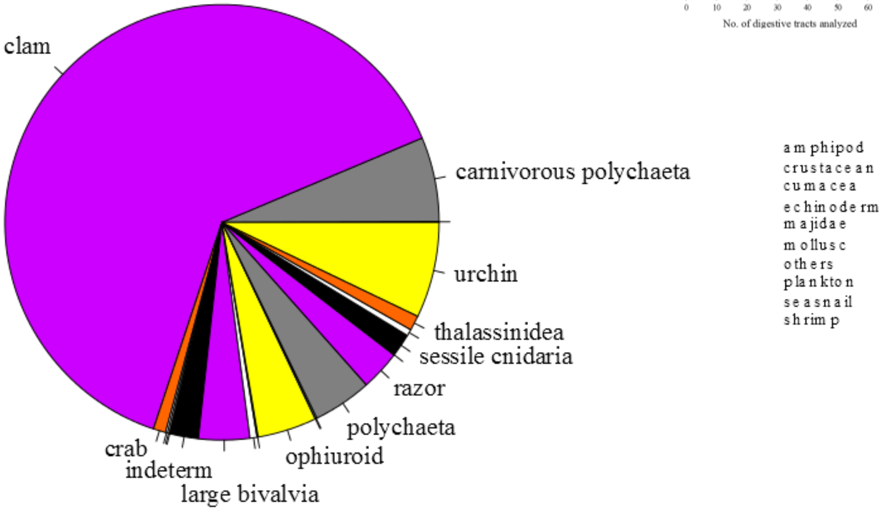
Plie / European plaice

Forme moyenne / mean shape



Régime alimentaire / diet   Courbe cumulée des proies / Cumulative prey curve

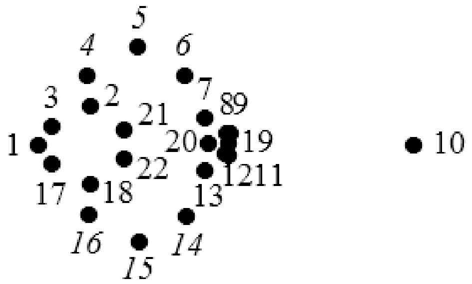




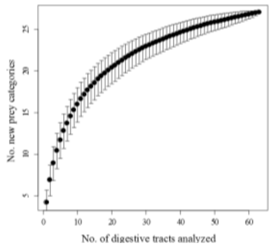
Raja clavata (Linnaeus, 1758) Elasmobranchii, Rajiformes, Rajidae

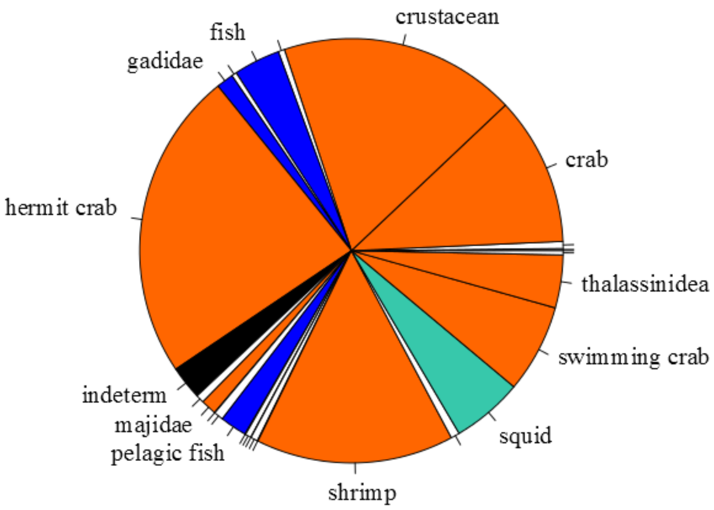
Raie bouclée / Thornback skate

Forme moyenne / mean shape



Régime alimentaire / diet Courbe cumulée des proies / Cumulative prey curve

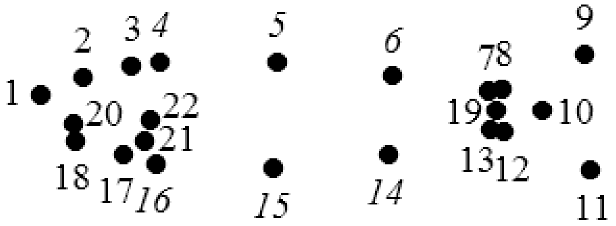




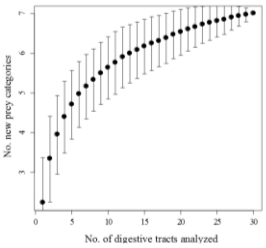
Sardina pilchardus (Walbaum, 1792) Actinopterygii, Clupeiformes, Clupeidae

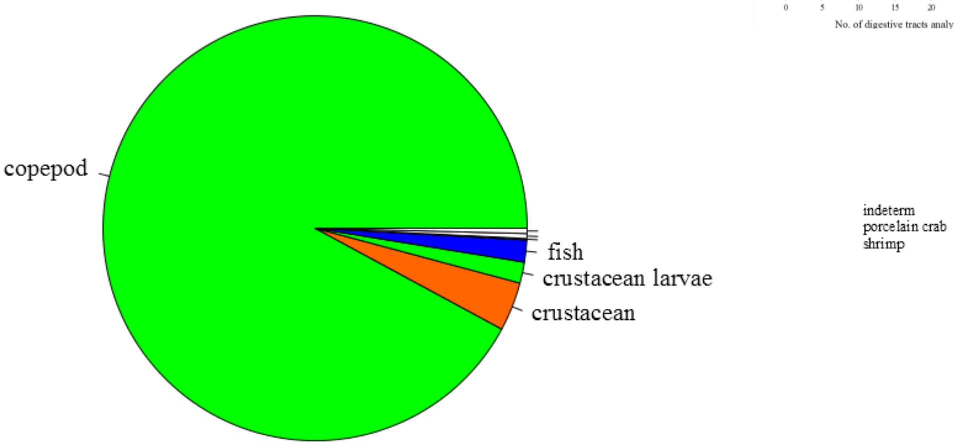
Sardine / European pilchard

Forme moyenne / mean shape



Régime alimentaire / diet Courbe cumulée des proies / Cumulative prey curve

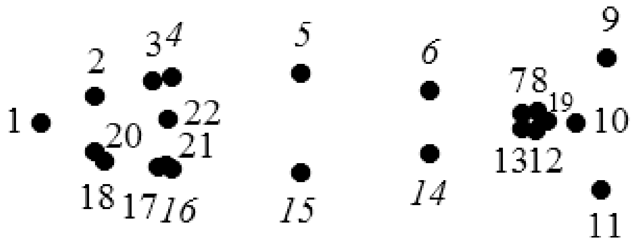




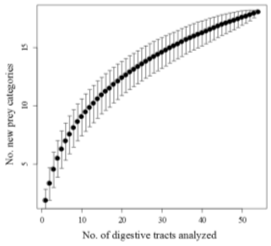
Scomber scombrus (Linnaeus, 1758) Actinopterygii, Perciformes, Scombridae

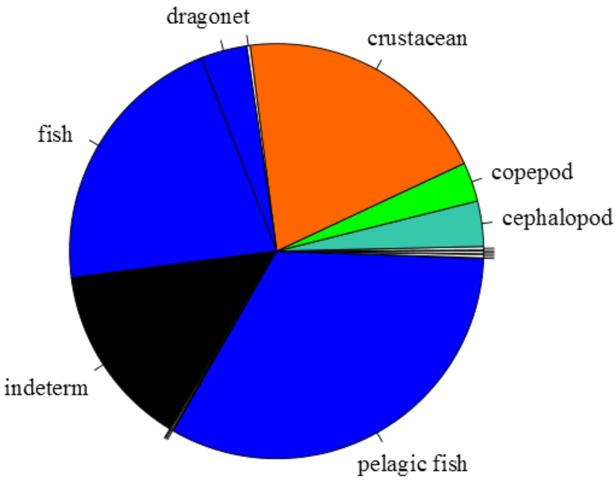
Maquereau / Atlantic mackerel

Forme moyenne / mean shape



Régime alimentaire / diet Courbe cumulée des proies / Cumulative prey curve

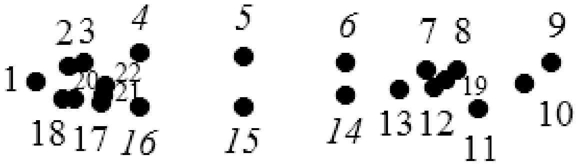




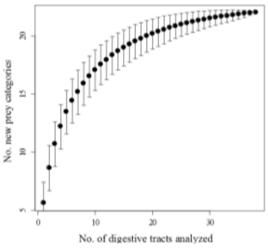
Scyliorhinus canicula (Linnaeus, 1758)   Elasmobranchii, Carcharhiniformes, Scyliorhinidae

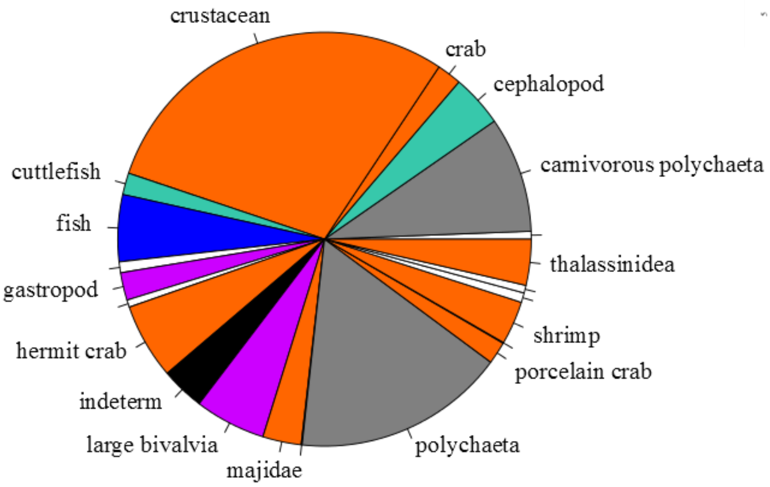
Petite roussette / Smallspotted catshark

Forme moyenne / mean shape



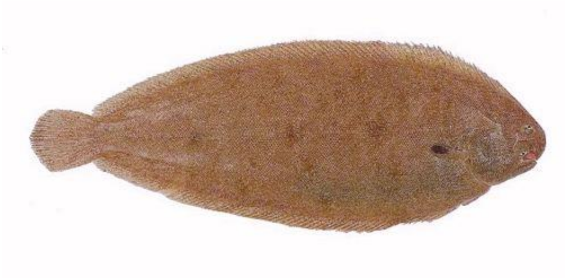
Régime alimentaire / diet   Courbe cumulée des proies / Cumulative prey curve



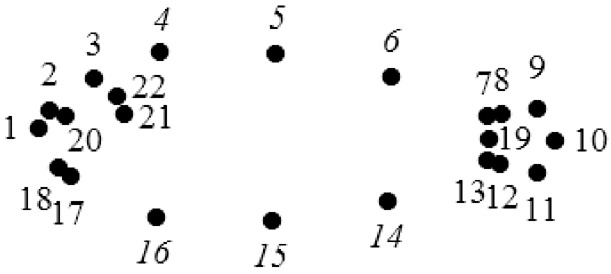


Solea solea (Linnaeus, 1758) Actinopterygii, Pleuronectiformes, Soleidae

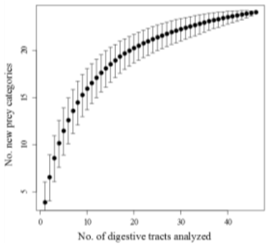
Sole commune / Common sole

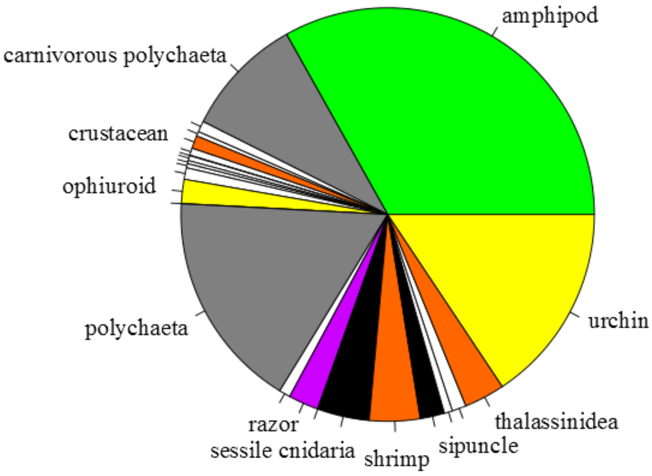


Forme moyenne / mean shape



Régime alimentaire / diet Courbe cumulée des proies / Cumulative prey curve

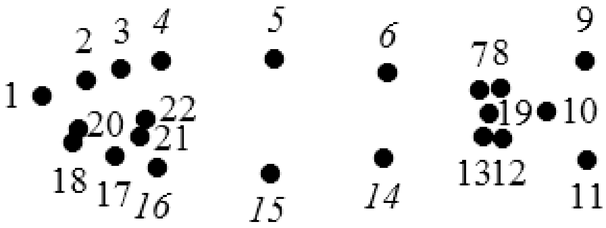




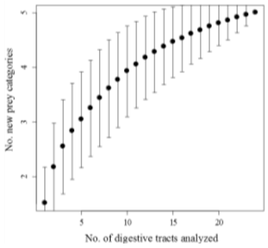
Sprattus sprattus (Linnaeus, 1758) Actinopterygii, Clupeiformes, Clupeidae

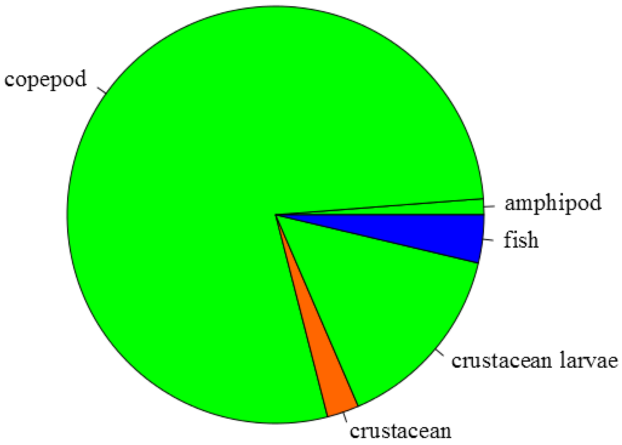
Sprat / European sprat

Forme moyenne / mean shape



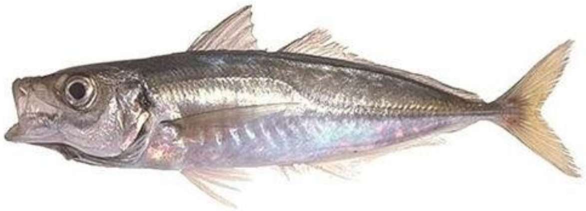
Régime alimentaire / diet Courbe cumulée des proies / Cumulative prey curve



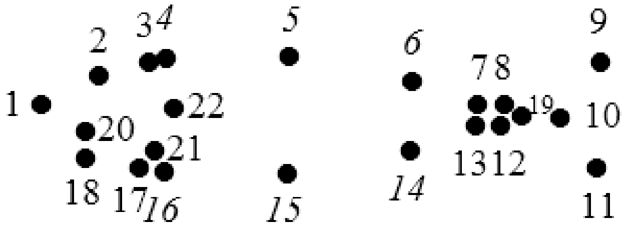


Trachurus trachurus (Linnaeus, 1758) Actinopterygii, Perciformes, Carangidae

Chinchard / Atlantic horse mackerel



Forme moyenne / mean shape



Régime alimentaire / diet Courbe cumulée des proies / Cumulative prey curve