FISHING IMPACTS ON THE TROPHIC FUNCTIONING OF MARINE ECOSYSTEMS,

A COMPARATIVE APPROACH USING TROPHODYNAMIC MODELS

by

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IMPACTS DE LA PÊCHE SUR LE FONCTIONNEMENT TROPHIQUE DES ÉCOSYSTÈMES MARINS − UNE APPROCHE COMPARATIVE BASÉE SUR DES MODÈLES TROPHODYNAMIQUES

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Abstract

Faced with the global overexploitation of marine resources and the rapid degradation of ecosystems' integrity, many states agreed to the principle of an ecosystem approach to fisheries (EAF). In fact, overfishing induces strong decrease of targeted species biomass, which impact predators, their competitors, prey, and ultimately the ecosystems' trophic networks. Thus, it is an important challenge to understand the trophic functioning of marine ecosystems and the related impacts of fisheries.

In this spirit, my thesis was developed to address concerns about the potential impacts of fisheries on the underlying trophic functioning, and to better understand this trophic functioning and its variability through ecosystems. Two well-known trophodynamic models were used: Ecopath with Ecosim (EwE) and EcoTroph (ET). First, I developed EcoBase, i.e., an online repository to gather and communicate information from EwE models, which enabled to give a global overview of the applications of the EwE modeling approach. Then, the ET model was corrected and standardized through the creation of a software package in R. A new trophic control, i.e., foraging arena (FA) trophic control, was integrated to study its impacts on trophic flows and fishing effects on aquatic ecosystem trophic networks. I showed that that making ecosystem behavior more realistic by incorporating FA controls into EcoTroph decreased the resistance and the production of modeled ecosystems facing increasing fishing mortality. An analysis of case studies focusing on marine protected areas (MPAs) was then performed using EwE and ET. I analyzed the potential spillover effect from three MPAs, and showed that their potential exports were at the same order of magnitude as the amount of catch that could have been obtained inside the reserve. Finally, a meta-analysis of marine ecosystem trophic

functioning was conducted using 127 EwE models, which showed that ecosystem types were distinguished by different biomass trophic spectra and associated trophic indices. These differences were mainly driven by different production, but also kinetic for some ecosystem types. In conclusion, trophodynamic models, as EwE and ET, appeared to be useful tools to better understand the trophic functioning of marine ecosystems, its variability through ecosystems, and the associated impacts of fisheries.

Résumé

Face à une situation mondiale de surexploitation des ressources et de dégradation de l'intégrité des écosystèmes marins, le développement de l'Approche Ecosystémique des Pêches est aujourd'hui reconnu comme une urgente nécessité. La pêche induit des diminutions souvent très importantes de l'abondance des espèces ciblées. Ces modifications, comme celles liées aux destructions d'habitats ou à la pollution, se répercutent via les réseaux trophiques à l'ensemble des communautés écologiques et au fonctionnement de l'écosystème. De plus, l'ampleur des impacts varie compte tenu du fonctionnement trophique des écosystèmes. Dans cette perspective, le développement d'approches comparatives à grande échelle et de modèles de fonctionnement trophique des écosystèmes sont identifiés comme des étapes clés afin d'analyser, quantifier et si possible prévoir l'impact de la pêche sur l'ensemble des compartiments des écosystèmes marins. L'un des principaux modèles écosystémiques aujourd'hui utilisés est le modèle EwE développé au sein de l'Université de Colombie Britannique. Ce modèle quantifie les flux trophiques entre les compartiments d'un écosystème. Il a fait l'objet de plusieurs centaines d'applications dans des situations extrêmement diverses. Le modèle EcoTroph, développé au sein de l'UMR ESE à Agrocampus Ouest, est quant à lui plus récent. Il conduit à une représentation théorique simplifiée du fonctionnement des écosystèmes aquatiques à travers l'utilisation de spectres trophiques.

De nouvelles connaissances sur le fonctionnement trophique des écosystèmes marins ont été acquises grâce à la modélisation écosystémique. En effet, de nombreux modèles EwE ont mis en évidence des modifications du fonctionnement trophique causées par l'impact de la pêche. Mais ces modèles sont hétérogènes et ne couvrent qu'une partie de l'océan. Réciproquement, le

modèle ET peut être "plaqué" sur un modèle EwE et constitue un cadre unifié de représentation à travers l'utilisation de spectres trophiques. Il permet d'identifier les paramètres clés du fonctionnement trophique : les efficiences de transfert trophique, la cinétique des flux de biomasse, l'impact des contrôles top-down… ET est également un outil de diagnostic des impacts de la pêche à l'échelle écosystémique. Il permet une approche générique et une extrapolation à l'échelle globale. Le travail de thèse s'inscrit à la convergence de ces deux approches EwE et ET, il s'appuie sur une approche comparative entre écosystèmes et vise ainsi à répondre aux questions suivantes :

- Quels sont les déterminants clés du fonctionnement trophique des écosystèmes marins ?

- Dans quelle mesure ces paramètres déterminent-ils des changements écosystémiques liés aux impacts de la pêche ?

  Cinq étapes ont été identifiées afin de répondre à ces questions :

- Création d'un répertoire d'informations (EcoBase) afin d'agglomérer les données provenant des modèles EwE, et de donner une vue d'ensemble des applications de ce modèle ;

- Révision et développement du modèle EcoTroph à travers l'inclusion de la « foraging arena theory » (théorie des aires de nourricerie), la création d'un package R, et une meilleure évaluation de la sensibilité des paramètres du modèle ;

- Utilisation de EwE et ET afin de réaliser une première méta-analyse portant sur les aires marines protégées (AMPs) et leurs exports potentiels de biomasse ;

- Synthèse et analyses comparatives de 127 modèles EwE disponibles dans EcoBase étant donnés différents types d'écosystème. ET est utilisé comme un outil de comparaison afin d'effectuer une méta-analyse du fonctionnement trophique des écosèmes marins.

L'accent est mis sur l'identification de fonctionnement type et des paramètres clés associés.

Ma thèse de doctorat est donc organisée en six chapitres. Le chapitre 1 présente une introduction générale décrivant le contexte de mon étude, mes questions de recherche et les principales raisons motivant de telles questions. Dans le chapitre 2, je présente EwE et EcoBase, c'est-à-dire un répertoire d'informations développé afin d'agglomérer et communiquer les données provenant des modèles EwE. Ces données nous ont permis de fournir un aperçu global des applications du modèle EwE. Dans le chapitre 3, je présente le modèle EcoTroph et les différentes améliorations que j'ai apportées, notamment l'intégration de la « foraging arena theory ». Le chapitre 4 présente une analyse portant sur trois cas d'études d'AMPs en utilisant EwE et ET afin d'estimer les exports potentiels de biomasse provenant des AMPs (effet « spillover »). Dans le chapitre 5, j'ai mené une méta-analyse du fonctionnement trophique des écosystèmes marins en utilisant 127 modèles EwE. Je me suis focalisé sur l'identification de fonctionnements trophiques types et de leurs paramètres clés associés. Enfin, le chapitre 6 résume mes conclusions et présente mes observations finales. Je discute également les possibles défauts et insuffisances des analyses effectuées, et fait des recommandations portant sur les futurs intérêts de recherche et les améliorations à apporter aux modèles écosystémiques.

Preface

I co-performed all data analysis presented in Chapter 2 with Audrey Valls (UBC Fisheries Centre, PhD candidate). I prepared and wrote Chapter 2 which is based on two publications that benefited from comments and edits by co-authors:

- Colléter M., Valls A., Guitton J., Morissette L., Arreguín-Sánchez F., Christensen V., Gascuel D., Pauly D. (2013) EcoBase: a repository solution to gather and communicate information from EwE models. Fisheries Centre Research Reports 21(1), 60p.

- Colléter M.*, Valls A.*, Guitton J., Gascuel D., Pauly D., Christensen V. (under review) Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase model repository. Submitted to Ecological Modelling, 08/22/2014 (*: co-first authors).

I also wrote a book chapter that combines these two publications and a study I did not contribute to (Christensen et al., 2014, 2011). This book chapter benefited from comments and edits by co-authors: Colléter M., Valls A., Christensen V., Gascuel D., Guitton J., Piroddi C., Coll M., Steenbeek J., Buszowski J., Pauly D. (in press) Modeling the global ocean with the Ecopath family of software; A brief review, with an application example. In: Pauly D., Zeller D. (eds.) Global Atlas of Fisheries: Ecosystem Impacts and Analysis. Island Press, Washington, D.C.

I performed all data analysis presented in Chapter 3. I prepared and wrote Chapter 3 which is based on two publications that benefited from comments and edits by co-authors:

- Colléter M., Guitton J., Gascuel D. (2013) An Introduction to the EcoTroph R Package: Analyzing Aquatic Ecosystem Trophic Networks. R Journal 5(1): 98-107.

- Colléter M., Walters C.J., Gatti P., Gascuel D. (under review) Foraging arena and top-down controls: impacts on modeling trophic flows and fishing effects on aquatic ecosystem trophic networks. Submitted to Marine Ecology Progress Series, 07/29/2014.

I prepared and wrote Chapter 4 which is based on a publication that benefited from comments and edits by co-authors. I performed all data analysis presented in this Chapter with the help of all co-authors: Colléter M., Gascuel D., Albouy C., Francour P., Tito de Morais L., Valls A., Le Loc'h F. (2014) Fishing inside or outside? A case studies analysis of potential spillover effect from marine protected areas, using food web models. Journal of Marine Systems 139: 383-395.

I prepared and wrote Chapter 5 as a manuscript which benefited from comments and edits by co-authors Gascuel D. and Pauly D. I performed all data analysis presented in this Chapter. All data analysis was performed on EwE models I gathered from three previously developed databases. Permission to use these data was provided by the three contributors: Morissette L., Arreguín-Sánchez F., and Christensen V.

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ABTS: Accessible biomass trophic spectra

AMP: Aire marine protégée

API: Application programming interface

BTS: Biomass trophic spectra

CBD: Convention on Biological Diversity

CPU: Central processing unit

CPUE: Catch per unit of effort

CRAN: Comprehensive R Archive Network

CTS: Catch trophic spectra

CTSA: Catch Trophic Spectrum Analysis

DBAs: Database administrators

EAF: Ecosystem approach to fisheries

EE: Ecotrophic efficiency

ERDC: Ecopath Research and Development Consortium

ET: EcoTroph

EUs: Expert users

EwE: Ecopath with Ecosim

FA: Foraging arena

FAO: Food and Agriculture Organization of the United Nations

GUs: General users

ICES: International Council for the Exploration of the Sea

ICLARM: International Center for Living Aquatic Resources Management

IPCC: Intergovernmental Panel on Climate Change

KTS: Kinetic trophic spectra

LIM: Linear Inverse Model

LM: Linear model

LME: Large marine ecosystem

MPA: Marine protected area

NA: Not available

NTE: Net transfer efficiency

ODBC: Microsoft Open Database Connectivity

OI: Omnivory index

PCA: Principal component analysis

POP: Persistent organic pollutants

PP: Primary production

PPR: Primary production required

p_{sust}:   Probability of an ecosystem being sustainably fished

PTS: Production trophic spectra

RDBMS: Relational Database Management System

SSR: Sum of squared residuals

SST: Sea surface temperature

TB: Total biomass

TE: Transfer efficiency

TL: Trophic level

TPP: Total primary production

TR: Total respiration

TST: Total system throughput

UBC: University of British Columbia

WSSD: World summit on sustainable development

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To my family, my friends, and Neil who left us much too young.

Chapter 1: General introduction

1.1 Trends in the status of world fisheries

After decades of increase in world fisheries catches, they reached a peak since the beginning of the 1990s, especially when taking into account the discards (Alverson et al., 1994), unreported catches and correction of China's over-reported catches (Watson and Pauly, 2001; Zeller and Pauly, 2005). A reduction of 0.66 million tonnes per year since 1988 in the global catches has been calculated by Watson and Pauly (2001), suggesting a decline in fisheries catches for the last 25 years at the world scale. At the same time, major concerns have been addressed regarding the state of exploited stocks. The last synthesis of the FAO on the state of world fisheries (FAO, 2014) indicated that the fraction of assessed stocks fished at a sustainable level decreased from 1974 to 2011 (from respectively 90 to 71.2%). More precisely, the underfished stocks decreased continuously, while the fully fished stocks decreased until 1989 and then increased to 61.3% in 2011. Simultaneously, the fraction of overexploited stocks increased from 10% in 1974 to 32.5% in 2008, and then declined slightly (28.8% in 2011). Overexploitation has been observed for all the different marine ecosystem components: demersal (e.g., Christensen et al., 2003b), pelagic (e.g., Beverton, 1990), deep sea (e.g., Koslow et al., 2000; Roberts, 2007), and large pelagic species (e.g., Myers and Worm, 2003), sharks and rays (e.g., Baum et al., 2003; Baum and Myers, 2004), or mollusks (e.g., Gillespie, 2009). All these elements reflect an historical overfishing that has been shown to be the first major disturbance to coastal ecosystems (Jackson et al., 2001). The overexploitation has a large impact on ocean resources and raised concerns about the sustainability of the fisheries activities (Coll et al., 2008; Pauly and Christensen, 1995; Pitcher and Cheung, 2013). Furthermore, fisheries activities

showed limitations with the collapse of nearly one fishery of four over the last 50 years (Mullon et al., 2005), the rapidly diminishing number of new fishing grounds (Swartz et al., 2010) and fish stocks (Froese et al., 2008). In fact, the increase in demand for seafood has led to a substantial expansion of fisheries through all the oceans and marine habitats (Pauly et al., 2002; Swartz et al., 2010), at all depths (Morato et al., 2006; Pauly et al., 2003), and toward lower trophic levels (Essington et al., 2006; Pauly et al., 1998).

1.2   Main fishing impacts on marine ecosystems

Fishing activities can modify marine resources by truncating the demographic structure of stocks leading to greater resource instability (Jackson et al., 2001), and by altering life traits such as mean body size and age at maturity (Olsen et al., 2004; Trippel, 1995). Thus, they have a direct impact on the biomass and the production of targeted species. Marine predators have been particularly affected by the fishing activities; a decline by more than a half since the 1950s has been predicted at a world scale (Tremblay-Boyer et al., 2011), and by two-thirds over the last hundred years, with 54% occurring in the last 40 years (Christensen et al., 2014). This phenomenon impacted the global marine ecosystem (Heithaus et al., 2008), and led, coupled with a reported effort on smaller trophic levels, to a decrease in the mean trophic level of the world catches, i.e. "fishing down marine food webs" (Pauly et al., 1998). Several case studies and analyses exhibited such a pattern with a strong decrease of predatory species biomass (e.g., Christensen et al., 2003b; Gascuel et al., 2014; Jennings et al., 2002a; Myers and Worm, 2003; Pinnegar et al., 2002). Fishing activities also impact habitats through seabed modification (Kaiser et al., 2002). These activities, combined with pollution and other anthropogenic disturbances can lead to depletions of marine resources and ecosystems (e.g., Le Pape et al.,

2007; Rochette et al., 2010). All the compartments of ecosystems are so potentially affected by fishing activities. Despite the fact that main targets are certain size/age groups of selected species, fishing takes place in an ecosystem context with unavoidable repercussions on predators, their competitors, prey, and ultimately the entire ecosystem's trophic network.

Several studies showed changes within trophic networks due to fishing impact. For instance, Shepherd and Myers (2005) reported declines in shallow water coastal elasmobranchs where shrimping effort was high, and increases in deeper water elasmobranchs due to an associated predation release; Estes and Palmisano (1974) showed that the removal of sea otters caused an increase of their former prey, sea urchins, resulting in sea urchin barrens (review in Baum and Worm, 2009). Thus, fishing can induce disruptions in top-down controls, i.e. controls exerted by a predator on its prey abundance or biomass (Paine, 1980), by the removal of predatory species, and impact ecosystem structure, functioning and resilience (Baum and Worm, 2009; Duffy, 2002; Paine, 1969). These effects may reach multiple trophic links, leading to trophic cascades (Andersen and Pedersen, 2010; Carpenter and Kitchell, 1993). Disruptions of food web dynamics are not uniform across ecosystems, and may vary according to the production characteristics of prey (Borer et al., 2005), and the targeted part of the ecosystem (Gascuel et al., 2011). There is no scientific consensus about the drivers behind top-down effects and how they change between systems (Baum and Worm, 2009; Borer et al., 2005; Frank et al., 2007; Gruner et al., 2008), but it is agreed that they can play an extremely important role in shaping ecosystem structure. It may be a major feature of ecosystem resistance to fishing, as suggested by modeling studies (e.g., Gascuel, 2005).

1.3   Main effects of climate change on marine ecosystems

Global climate change is currently affecting marine and terrestrial ecosystems (Halpern et al., 2008; Parmesan and Yohe, 2003; Walther et al., 2002). Mean air temperature increased by 0.8°C since 1900, and 10 record temperatures have been observed since the last 12 years (IPCC, 2007). This global phenomenon is expected to continue to disturb and change our ecosystems as global mean air temperature is predicted to increase at a rate of 0.2 to 0.4°C per decade during this century (IPCC, 2013, 2007). Global warming simulations predict large changes in environmental and physical conditions in the ocean: oceanic temperature and sea level increases, changes in vertical stratification, ocean circulation, surface winds, upwelling, cloudiness and sea ice, and thus light supply to the surface ocean (Bakun, 1990; IPCC, 2013, 2007; Sarmiento et al., 2004). Ocean biogeochemical properties are also affected, such as the salinity (Sarmiento et al., 2004), the pH, oceans becoming more acidic (IPCC, 2013, 2007; Riebesell et al., 2009), the oxygen content (Cheung et al., 2012), or the presence of aerosol deposition (Paytan et al., 2009).

Such changes will cause strong alterations in the biology of oceans and marine resources. Climate change has direct and indirect impacts on marine organisms. Direct effects act on physiology, growth, mortality, reproductive capacity, populations dynamics and geographic distributions (Brander, 2007; Harley et al., 2006; Pauly, 2010, 1980; Perry et al., 2005; Pörtner and Farrell, 2008). Marine species respond to ocean warming by shifting their latitudinal range (Beaugrand et al., 2002; Cheung et al., 2009; Hiddink and Ter Hofstede, 2008; Perry et al., 2005) and depth range to cooler waters (Dulvy et al., 2008). Such species responses may lead to local extinction and invasions, resulting in changes in the pattern of marine biodiversity and ecological disturbances (Cheung et al., 2009; Worm et al., 2006). Indirect effects alter the productivity, structure and composition of the ecosystem (Brander, 2007; Brown et al., 2010; McGowan et al.,

1998). Such impacts potentially affect ecological interactions, food web structure and trophic functioning (Poloczanska et al., 2008; Preston et al., 2008). Ocean acidification could affect marine organisms' calcification and increase the physiological stress (Iglesias-Rodriguez et al., 2008; Orr et al., 2005; Pörtner and Farrell, 2008), and reduced oxygen content shrink body size of marine fishes (Cheung et al., 2012). Several studies highlighted the potential impact of increasing sea surface temperatures on primary production (Behrenfeld et al., 2006; Sarmiento et al., 2004). All these elements raise concerns about changes on global fisheries potential (Blanchard et al., 2012; Cheung et al., 2010), and, concomitantly, if such changes can meet fish demand from a growing population in relation to fisheries management (Merino et al., 2012).

1.4 Developments in the study of marine ecosystem trophic functioning

Trophic functioning is a well-studied scientific area. Processes taking place in aquatic ecosystems have been explored and defined since several decades (e.g., Elton, 1927; Graham and Edwards, 1962; Gulland, 1970; Lindeman, 1942; Moiseev, 1969; Ryther, 1969; Schaefer, 1965). The common reasoning is based on the ecosystem concept, "defined as the system composed of physical-chemical-biological processes active within a space-time unit of any magnitude, i.e., the biotic community plus its abiotic environment" (Lindeman, 1942). Within this ecosystem, trophic dynamics can be seen as energy transfers from one part to another, defining qualitative and quantitative food-cycle relationships. Different processes impact the ecosystem functioning such as predation, ontogeny processes, natural mortality; and also more precise food-cycle energetic views as production, consumption, loss through respiration, unassimilated consumption (Lindeman, 1942). There are several ways to define and represent an ecosystem. One widely used approach is based on the trophic level concept. Elton (1927) and Lindeman (1942)

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introduced this concept for describing aquatic ecosystems by assigning integer trophic levels (TLs) to the individual numbers, to the biomass or to the biological production by its component species. This approach differentiated between primary producers and detritus (TL=1), first-order consumers (TL=2), second-order consumers (TL=3), etc… The ecosystem is so represented as a pyramid of number, biomass or production, from low to high TLs. Odum and Heald (1975) developed this concept by implementing fractional trophic levels resulting from the diet of the individual and the trophic level of its prey organisms.

This highlighted the primary production as a base of energy production surging up the food web with losses at each level. This development led to interesting work linking the photosynthesis and the fish biomass in marine ecosystems (Graham and Edwards, 1962; Gulland, 1970; Moiseev, 1969; Ryther, 1969; Schaefer, 1965), based on primary production, food-chain length and ecological efficiency data. These studies were shown to be based on guesses and several pitfalls in the methods (Alverson et al., 1970; Pauly, 1996). However, food-chain length and the ecological efficiency parameter are noteworthy, as they are directly linked to trophic functioning. Food-chain length defines the number of levels required for "the transfer of organic matter from the photosynthetic organisms to fish and invertebrate species" (Ryther, 1969). Ecological efficiency (or transfer efficiency; TE), defines the rate of energy entering a trophic level that is transferred to the next trophic level (Lindeman, 1942). Numerous approaches have been suggested for calculation of this key parameter (Jennings et al., 2002b; Lindeman, 1942; Pauly and Christensen, 1995), used in ecosystem modeling and calculations of ecosystem indices (e.g., p_{sust}, Libralato et al., 2008; PPR, Pauly and Christensen, 1995). These breakthroughs showed the need for a better understanding of aquatic ecosystem functioning and the underlying trophic networks to assess fishery impacts. It led to a great number of food web model

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approaches (Whipple et al., 2000). Many indicators derived from the TL concept are now commonly used by the scientific community, thanks to their ability to reveal ecosystem-level patterns (e.g., Cury et al., 2005; Shannon et al., 2014).

1.5   Toward an ecosystem approach to fisheries (EAF)

Despite numerous insights into trophic functioning, fishing ecosystem effects are still unaccounted for by a predominant use of single-species assessments in fisheries regulation (Jennings and Kaiser, 1998). It has been showed that optimizing exploitation of all species separately and simultaneously is impossible (Walters et al., 2005), and management based on the preservation of each spawning stock biomass is misleading when considering interspecific interactions (Gislason, 1999). Single-species models do not account for trophic interactions of major importance as predation and competition (Larkin, 1963). Several multispecific models have been developed (e.g., Andersen and Ursin, 1977; May et al., 1979), and also food web models (e.g., Ecopath; Christensen and Pauly, 1992; Polovina, 1984). The scientific community claimed for the implementation of an ecosystem dimension in fisheries management (e.g., Botsford et al., 1997; Pikitch et al., 2004). Principles of ecosystem management have been clearly identified and formulated (Christensen et al., 1996; Lackey, 1998).

This led to the emergence of a new concept, the ecosystem approach to fisheries (EAF). It aimed to place fisheries in their ecosystem context, and to emphasize the link between human welfare and ecosystems health (Garcia et al., 2003; Sinclair et al., 2002). A basis for EAF was provided by the adoption a "Code of conduct for responsible fisheries" by the FAO in 1995 (FAO, 1995). It stated that "the right to fish carries with it the obligation to do so in a responsible manner so as to ensure effective conservation and management of the living aquatic resources".

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This approach has then been officially recognized during the world summit on sustainable development (WSSD) plan of implementation. It committed countries to a better management of natural resources (WSSD, 2002). EAF has been detailed with governance and management guidelines to enable its implementation by authorities (Garcia et al., 2003). However, a major difficulty is the transposition of such guidelines into operational management decisions. This approach must adapt considering the ecosystems diversity, and considerable work is still needed to replace conventional approaches by ecosystem management accounting for the three pillars of sustainable development, i.e., economic development, social development and environmental protection (Garcia and Cochrane, 2005). The move toward an EAF calls for a scientific support to answer queries by management stakeholders. Ecosystem modeling is an important tool for the evaluation of scenarios and trade-offs, and to explore further the trophic functioning of marine ecosystems (Plagányi, 2007).

1.6   The use of trophodynamic models

Ecosystem models can be a strategic tool of ecosystem-based management (Plagányi, 2007; Sainsbury et al., 2000). Several ecosystem models, such as Ecopath with Ecosim (Christensen and Pauly, 1992; Christensen and Walters, 2004), OSMOSE (Shin and Cury, 2004, 2001), size spectra (Jennings et al., 2008), Atlantis (Fulton et al., 2011), or Linear Inverse Model (LIM; Niquil et al., 2011; Vézina and Piatt, 1988), have been applied to an increasing number of marine ecosystems. Each model is based on different assumptions and hypotheses, and represents only one of many possible visions of an ecosystem (Wolff, 2002). These models use various kinds of derived indicators to inform the user about the ecosystem's state and the impacts of fishing or environmental disturbances (e.g., Blanchard et al., 2005; Link, 2002; Niquil et al.,

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2012; Shannon et al., 2014; Ulanowicz, 1986). Ecosystem modeling is an active field of research with an approximately 20% growth rate per year in the annual number of model publications since 1995. More than a half of these publications are related to the EwE modeling approach (Christensen and Walters, 2011).

The emergence of EwE as a widely used approach and software for modeling aquatic ecosystems is due to its relative long history, its free availability and an extended support (Christensen and Walters, 2011). EwE relies on the description of ecosystems in terms of trophic groups and flows connecting them. The trophic groups represent biological components pooled together according to similarities of species trophic properties and distribution. Biomass flows within groups are mass-balanced, such that consumption by a group is sufficient to account for its respiratory losses, biomass growth or decline and biomass production. Flows between groups are also balanced so that each group's biomass production is sufficient to account for consumption by its predators and fishery catches (see details in Section 2.3). A dynamic version (Ecosim) has been added to explore past and future impacts of fishing and environmental disturbances on trophic networks (Christensen and Walters, 2004). EwE model was applied on hundreds of case studies covering a wide diversity of ecosystems type and size (Morissette, 2007). EwE also contributed in a major way to the reemergence of the trophic level concept (Lindeman, 1942; Odum and Heald, 1975), especially as TLs were not an input to EwE, but an estimated parameter resulting from the species' diets (see details in Section 2.3).

EcoTroph (ET), a recent approach and software for modeling marine and freshwater ecosystems, is articulated entirely around the TL concept. It has been developed at the same time as the EwE worldwide expansion, and incorporated into the EwE plug-in family (Gascuel, 2005; Gascuel and Pauly, 2009). The trophic functioning of aquatic ecosystems is modeled as a

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continuous flow of biomass surging up the food web, from lower to higher TLs, through predation and ontogenic processes (see details in Section 3.3). Such an approach, wherein species as such disappear, may be viewed as the final stage in the use of the TL metric for ecosystem modeling. It provides a simplified but useful representation of ecosystem functioning and impacts of fishing. ET has been used either in theoretical contexts based on virtual ecosystems (Gascuel et al., 2011; Gascuel and Pauly, 2009), or in specific case studies to assess the current fishing impacts at the ecosystem scale in the South African Benguela ecosystem (Gasche et al., 2012), in the Bay of Biscay (Lassalle et al., 2012), for a worldwide analysis (Tremblay-Boyer et al., 2011), to analyze the effects of marine protected areas on the whole food web (Senegal, Colléter et al., 2012; Mediterranean Sea, Valls et al., 2012), or to estimate the mesopelagic fishes biomass in the open ocean (Irigoien et al., 2014). Furthermore, it enables the construction of a unique framework for EwE models comparison, the trophic spectrum. This display, based on the ET key ideas, is a graphical representation of the ecosystem parameters along the trophic level (Gascuel et al., 2009b, 2005). These two trophodynamic models were used in my thesis, which is now presented.

1.7 Research objectives

Fishing activities induce declines in targeted species' biomass. These changes, coupled with habitat destructions, climate change, and pollution, affect entire ecosystem via its trophic network. The magnitude of impacts varies according to ecosystem trophic functioning. New insights into trophic functioning have been made possible thanks to ecosystem modeling. Indeed, several EwE models highlighted modifications into ecosystems trophic functioning caused by fishing activities (e.g., Coll et al., 2009). EwE models are structurally different and their global

extent is limited. However, EcoTroph constitutes a unique comparison framework through the use of trophic spectra. It enables the identification of trophic functioning key parameters: trophic transfer efficiencies and flow kinetics, top-down control impacts… ET is also a diagnosis tool regarding ecosystem fishing impacts. It enables a generic approach and an extrapolation at a global scale. The proposed research aims to answer the following questions:

- What are the key determinants of ecosystem trophic functioning?

- To what extent do these parameters determine ecosystem changes given fishing impacts?

Five general steps were distinguished in the proposed research:

- Creation of a repository to gather information from EwE models and give a global overview of the applications of this modeling approach;

- Revision and development of the EcoTroph model through the implementation of the foraging arena theory, the creation of an R-package, and a better assessment of parameters sensitivity;

- Use of EwE and ET to perform a first meta-analysis focusing on MPAs and their potential biomass exports;

- Synthesis and comparative analyses of 127 EwE models available in EcoBase (EwE model repository) considering different ecosystem types. ET is used as a comparison tool to carry out a meta-analysis of marine ecosystems trophic functioning. Focus will be put on the identification of typical functioning and the associated key parameters;

Thus, my thesis is organized into six chapters. Chapter 1 provides a general introduction outlining the background to my study, my research questions and the main motivations behind my study. In Chapter 2, I present Ecopath and EcoBase, i.e., an online repository to gather and communicate information from EwE models. This enabled to give a global overview of the

applications of the EwE modeling approach. In Chapter 3, I present the EcoTroph model and the different improvements I have made, notably the integration of foraging arena controls. In Chapter 4, I then performed an analysis of case studies focusing on marine protected areas (MPAs) using EwE and ET. I analyzed the potential spillover effect from three MPAs. In Chapter 5, I conducted a meta-analysis of marine ecosystem trophic functioning using 127 EwE models. I focused on the identification of typical trophic behaviors and the associated key parameters. And finally in Chapter 6, I summarize my findings and present my concluding remarks. I also discuss possible caveats in my research and make recommendations for future research focus and model refinements.

Chapter 2: Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase model repository

2.1 Summary

The 'Ecopath', later expanded to 'Ecopath with Ecosim' modeling approach (jointly 'EwE') have been applied to hundreds of ecosystems around the world. The 'EcoBase' model repository was developed to gather EwE models published worldwide. For the 435 unique models documented in EcoBase, all available metadata were compiled, standardized, and analyzed. Based on the year of publication of the models, the evolution of the EwE applications over the past thirty years was also analyzed. Overall, most models were built to analyze ecosystem functioning and fisheries, principally in the Northern and Central Atlantic Ocean. Half of the models were applied to tropical systems, while more than a third was used to perform time dynamic simulations. During the first decade of its development (1984-1993), most EwE applications were Ecopath models representing tropical marine systems, with a simple trophic structure. Over the past two decades (1994-2014), EwE models were applied to a wider variety of ecosystems, including polar regions and terrestrial systems, and to wider range of research topics, including pollution, aquaculture and marine protected areas. The modeling practices also evolved towards Ecopath models with larger spatial scales, shorter temporal scales, and more complex trophic structures. Over the past 30 years, the numbers of both publications and modelers have steadily increased, while the proportion of journal articles presenting EwE-based studies has been growing. This global and synthesized overview showed that the usage of and

interest for the EwE modeling approach in the scientific community had expended over the past three decades.

2.2   Introduction

The Life Sciences have reached a new era, that of the 'Big New Biology' (Thessen and Patterson, 2011). Ecology is following a similar path, and has turned into a 'data-intensive science' (Kelling et al., 2009; Michener and Jones, 2012). Ecological studies are more and more based on data-driven methodologies, relying on large pre-existing datasets and allowing for new insights on complex or underlying phenomena at global scales (e.g., Christensen et al., 2009).

A popular example of open-access, digital and cross-disciplinary datasets in aquatic ecology is FishBase, the online encyclopedia of fishes (www.fishbase.org). However, extensive data sharing is still rare in Life Sciences, and ecology has not yet joined the other historical "big" sciences, such as oceanography, meteorology or astronomy, where massive data-sharing is the norm (Edwards et al., 2010; Pauly, 1995; Thessen and Patterson, 2011). The open-access principle of sharing information online for free has been increasingly applied to publications, but much less to data, mainly due to issues with recognition and sense of data ownership (Thessen and Patterson, 2011; Vision, 2010). Although incentives for digitization of non-digital materials have been growing, existing repositories were estimated to represent less than 1% of the data in ecology (Reichman et al., 2011; Thessen and Patterson, 2011).

Data sharing is a required principle for independent verification and reuse (Vision, 2010), and published papers which make their data available are cited more frequently (Piwowar et al., 2007). Also, extensive data sharing may solve – at least in part – the problem of data loss, such as hard-copies or computer files in outmoded format (Zeller et al., 2005). Yet, sharing data is not

a tradition in ecology and faces sociological and technological obstacles (Hampton et al., 2013; Reichman et al., 2011; Thessen and Patterson, 2011). New practices are needed to make data sharing fully part of the culture in Life Sciences (Dalgleish et al., 2012; Hampton et al., 2013; Pauly, 1988; Reichman et al., 2011; Thessen and Patterson, 2011; Vision, 2010). The two critical stages at which practices have to be improved to allow for data sharing are the very first, i.e., the collection of the data, and the very last, i.e., their publication. Most of the time, biological data are not being collected with reuse in mind and are then published in a narrative or summarized style in scientific articles (Thessen and Patterson, 2011; Vision, 2010). The actual data are meant to be provided in online supplements or upon individual requests sent to the authors, but these options often remains unreliable (Vision, 2010).

While facing the challenges described above, ecology is more and more relying on modeling-based approaches to inform management. In aquatic ecology, the Ecopath with Ecosim modeling approach has been widely applied to inform ecosystem-based management (e.g., Christensen and Walters, 2011; Coll and Libralato, 2012; Jarre-Teichmann, 1998; Plagányi and Butterworth, 2004), since its original development in the early 1980s (Polovina, 1984). The EwE modeling approach was primarily developed as a tool-box to help fisheries management and answer 'what if' questions about policy that could not be addressed with single-species assessment models (Christensen and Walters, 2011, 2004; Pauly et al., 2000). Details on the core principles and equations of EwE can be found in the Section 2.3, and in the EwE user guide available online (Christensen et al., 2008). The EwE software is user-friendly, free (under the terms of the GNU General Public License) and downloadable online (www.ecopath.org). Thus,

hundreds of EwE models representing aquatic (but also some terrestrial) ecosystems have been developed and published worldwide.

By summarizing the available knowledge on the modeled ecosystems and deriving various system properties, EwE-based studies help understanding the structure and functioning of ecosystems, and thus may be seen as an important source of data (Walters et al., 1997). Indeed, building an EwE model require the collection, compilation and harmonization of various types of information: descriptive data on species abundance, diet composition and catch; computed data on species production, consumption and ecosystem properties; and simulation data on species biomass trends, after applying alternate scenarios. Several meta-analyses, based on a selection of EwE models, have been performed, focusing either on theoretical ecology and ecological concepts (e.g., Arreguín-Sánchez, 2011; Christensen and Pauly, 1993a; Gascuel et al., 2008; Pérez-España and Arreguín-Sánchez, 2001, 1999), or on ecosystems and species of particular interest (e.g., Christensen et al., 2003a, 2003b; Pauly et al., 2009). However, only few meta-analyses based on a large collection of EwE models have been published (e.g., Christensen, 1995; Christensen et al., 2014; Coll et al., 2013; Heymans et al., 2014, 2011; Morissette, 2007; Pikitch et al., 2014).

No comprehensive, open-access, digital collection of EwE models has been made previously, and this is why EcoBase was created. EcoBase is an online information repository of EwE models published in the scientific literature, developed with the intention of making the models discoverable, accessible, and reusable to the scientific community (http://sirs.agrocampus-ouest.fr/EcoBase/). Details on the structure, usage and capabilities of EcoBase can be found in Appendix A, and in the report introducing EcoBase available online

(Colléter et al., 2013b). The main goals of EcoBase are to (i) provide a comprehensive and up-to-date list of published EwE models and EwE-based applications; (ii) compile and present information from the referenced EwE models; (iii) facilitate future meta-analyses based on EwE models. Indeed, on top of detailed information on the modeled species and food web, each EwE-based study also provides a general description of the modeled ecosystem, which represents critical information required to reuse the model when conducting a meta-analysis. EcoBase offers a framework where this information may be stored, in a standardized and granular fashion, so that they can be reused as criteria based on which models can be selected for future meta-analyses.

In this chapter, EcoBase was used to compile available critical metadata on all the EwE models referenced in the model repository. First, the core principles and equations of EwE are presented. Then, EwE metadata were analyzed to propose a global and synthesized overview of the applications of the EwE modeling approach in the scientific literature. The focus is put on the objectives of the EwE-based studies, the complexity and scope of the models, the general characteristics of the modeled ecosystems, and the associated publication(s). Based on the year of publication of the models, the evolution of the EwE applications over the past thirty years was also analyzed. Results provided new insights on past and recent usage of and interest for the EwE modeling approach in the scientific community.

2.3   Ecopath with Ecosim core principles and equations

The foundation of the EwE modelling approach is an Ecopath model, which creates a static mass-balanced snapshot of the resources in an ecosystem and their interactions, represented by trophically linked functional groups. Thus, the modeled food web is represented

by functional groups, which can be composed of species, groups of species with ecological similarities, or ontogenetic fractions of a species. For each group, the Ecopath software solves two balancing equations: one to describe the production (Eq. (2.1)) and one for the energy balance (Eq. (2.2)).

$$B_i \times \left(\frac{P}{B}\right)_i = \sum_{j=1}^{N} B_j \times \left(\frac{Q}{B}\right)_j \times DC_{ji} + \left(\frac{P}{B}\right)_i \times B_i \times (1 - EE_i) + Y_i + E_i + BA_i \qquad (2.1)$$

$$Q_i = P_i + R_i + UA_i \qquad (2.2)$$

where N is the number of functional groups in the model, B the biomass, P/B the production rate, Q/B the consumption rate, DC_{ji} the diet composition representing the fraction of prey i in the diet of predator j, E the net migration rate, BA the biomass accumulation, Y the catches, EE the ecotrophic efficiency, i.e. the fraction of production which is used in the system, R the respiration, P the production, Q the consumption, and UA the unassimilated consumption because of egestion and excretion. The quantity $(1 - EE) \times P/B$ is the 'other mortality' rate unexplained by the model.

Thus, the Ecopath model assumes the trophic network to be in a steady state during the studied period, and consequently a mass-balance where the production of the group is equal to the sum of all predations, non-predatory losses, exports, biomass accumulations and catches (see Eq. (2.1)). Assuming there is no export and no biomass accumulation, and the catches Y are known, only three of the four parameters B, P/B, Q/B and EE have to be set initially for each group. Ecopath software computes mass-balance by solving the system of equations for the unknown parameters of all groups. The diet composition of each group is also required, i.e., the percentage of the prey items in the diet of the group (DC_{ji}). This enables Ecopath to calculate the

trophic level of each group (Eq. (2.3)), which characterizes their position within ecosystem's food web (Lindeman, 1942; Odum and Heald, 1975):

$$\tau_j = 1 + \sum_i \left(DC_{ji} \times \tau_i \right) \tag{2.3}$$

where τ_j is the TL of predator j and τ_i the TL of its prey. The trophic level of primary producers and detritus is conventionally set equal to 1.

A dynamic version, i.e., Ecosim, has been added to explore past and future impacts of fishing and environmental disturbances on trophic networks (Christensen and Walters, 2004). Ecosim is based on an Ecopath model, whose static mass-balanced equations provide some of the initial-state Ecosim parameters. It uses a system of time-dependent differential equations from the baseline mass-balance Ecopath model to describe the changes in biomass and flow of biomass within the system over time, by accounting for changes in predation, consumption and fishing rates (Christensen et al., 2005; Pauly et al., 2000; Walters et al., 2000, 1997). Thus, the biomass growth rate over time is expressed as (Eq. (2.4)):

$$\frac{dB_i}{dt} = g_i \times \sum_{j=1}^{N} Q_{ji} - \sum_{j=1}^{N} Q_{ij} + I_i - (M_i + F_i + e_i) \times B_i \tag{2.4}$$

where g_i is the net growth efficiency of prey pool i; Q_{ji} is the consumption by biomass pool i of all other pools j, Q_{ij} is the consumption of biomass (prey) pool i by other pools j; I_i is the immigration flow; M_i is the natural non-predation mortality rate; F_i is the fishing mortality rate; e_i is the emigration rate; and B_i is the biomass of the prey pool i. Calculations of consumption rates (Q_{ij}) are based on the 'foraging arena' theory (see Section 3.4.1), in which it is assumed that spatial and temporal restrictions in predator and prey activity cause partitioning of each prey population into vulnerable and invulnerable components (Ahrens et al., 2012; Walters et al., 1997; Walters and Juanes, 1993; Walters and Korman, 1999). The latest released version of EwE

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(version 6.4; Christensen et al., 2008) consists of a suite of three main routines: (i) Ecopath; (ii) Ecosim; and (iii) Ecospace, a spatial and temporal dynamic module based on Ecosim equations, and primarily designed for exploring impact and placement of marine protected areas (Christensen and Pauly, 1992; Christensen and Walters, 2004; Pauly et al., 2000; Walters et al., 1999).

2.4 Materials and methods

2.4.1 Compilation of the metadata in EcoBase

In EcoBase, an inventory of all EwE models published from 1984 to 2014 was completed (see Appendix A). This inventory intended to be as exhaustive as possible, although some models may be missing, especially if they were published after October 2013 (date of the publication of the EcoBase repository; Colléter et al., 2013b). The EwE modeling approach and software consists of a suite of three models: Ecopath, Ecosim, and Ecospace. In EcoBase, 'EwE models' primarily designate Ecopath models, based on which Ecosim or Ecospace models may have been developed later on.

Since three existing databases of EwE models were merged into the new EcoBase models repository (see Appendix A), some duplicates were obtained. A list of 435 'unique' models was extracted from the 573 models registered in EcoBase. Unique models were defined by the ecosystem they represent (i.e. the model area), the time period they cover (i.e. the model start and end years), and the author of the model (i.e. commonly the first author on the first publication based on the model). Thus, if several models represented the same ecosystem but for older or more recent time periods, over smaller or larger areas, or were developed by different

modelers, then they were considered as unique. The models representing the same ecosystem, but for different time periods, were specifically identified as 'replicates'. Most of the time, replicates were built by the same author and had the same number of groups, although there were some exceptions. The analyses presented in this study are based on the 435 unique EwE models documented in EcoBase. For each of the 435 models, all available metadata were compiled, standardized and encoded in EcoBase. Then, the metadata describing (i) the research objectives of the EwE-based studies, (ii) the structure, scales and units of the models, and (iii) the characteristics of the modeled ecosystems were analyzed (Table 2.1).

Table 2.1 List of the metadata (in alphabetical order) that were used in this study, and corresponding fields in EcoBase.

Metadata	EcoBase field	Definition
Aquaculture	aquaculture	Was the model developed to analyze aquaculture impact? (TRUE/FALSE)
Area	area	Model area (in km²)
Currency unit	currency_units	Currency unit of the model, e.g., wet weight, in t.km^{-2}
Ecopath	ecopath	Is the Ecopath routine used? (TRUE/FALSE)
Ecosim	ecosim	Is the Ecosim routine used? (TRUE/FALSE)
Ecospace	ecospace	Is the Ecospace routine used? (TRUE/FALSE)
Ecosystem	ecosyst_functioning	Was the model developed to analyze ecosystem functioning/structure? (TRUE/FALSE)
Ecosystem type	ecosystem_type	Type of the modeled ecosystem
Ecotracer	ecotracer	Is the Ecotracer plug-in used? (TRUE/FALSE)
EcoTroph	ecotroph	Is the EcoTroph plug-in used? (TRUE/FALSE)
Environment	environment_variability	Was the model developed to analyze environmental variability impact? (TRUE/FALSE)
Fisheries	fisheries	Was the model developed to analyze fisheries impact? (TRUE/FALSE)
Geographic extent	geographic_extent	Spatial polygon of the model (in decimal degrees)
Keystoneness	keystone_analysis	Is the Keystoneness tool in the Network Analysis plug-in used? (TRUE/FALSE)
Model	model_number	Model number (3-digits code) as recorded in EcoBase
MPA	mpa	Is the modeled ecosystem a MPA? (TRUE/FALSE)
Number of groups	number_groups	Number of functional groups included in the model
Pollution	pollution	Was the model developed to analyze pollution impact? (TRUE/FALSE)
Publication	id_ref	Publication number (3-digits code) as recorded in EcoBase
Publication	xml_ref	Reference in xml format (including year of publication, first author, and reference type)
Reference	referenced	Is the reference of the model recorded in EcoBase? (TRUE/FALSE)
Reference	ref_importance	Importance of the reference (1 by default)
Replicates	overlapping_code	Model number(s) of the replicate(s) (if several, noted as 195_196)
Replicates	overlapping_model	Are there other models representing the same ecosystem but over a different time period? (TRUE/FALSE)
Species	species_of_interest	Has the model been built to study a particular species/group? (TRUE/FALSE)

Metadata	EcoBase field	Definition
Stanzas	stanza_groups	Are there any stanzas in the model? (TRUE/FALSE)
Time period	model_year_end	End year of the model time period
Time period	model_year_start	Start year of the model time period
Time unit	time_units	Time unit of the model
Version	ewe_version_original	Version of EwE used by the modeler, as mentioned in the reference

In parallel, a comprehensive literature review was conducted, and 398 publications presenting EwE-based studies were compiled. The detailed references of these publications were encoded in EcoBase. Some of the information comprised in the references was used as metadata: the name of the first author; the year of publication; and the type of publication. Five publication types were considered: journal articles, reports (entire report and report sections), book sections, theses, and conference papers. For journal articles, the number of publications by scientific journal was also analyzed based on the title of the journals. Each of the 435 EwE models was associated to its corresponding publications. One model could have been described in more than one publication. In that case, the publications were classified as primary, secondary or tertiary reference, based on the year of publication and the level of details on the Ecopath model provided in the publications. Each model was associated to at least one reference. When several references were available for one model, the primary one was used to define the year of publication of the model. Then, the models were aggregated, based on their year of publication, into three groups corresponding to the past three decades (1984-1993; 1994-2003; 2004-2014), so as to analyze the evolution of EwE applications over time. Note that the same publication may describe multiple EwE models, so that only 398 publications were obtained for 435 models. All data used in this study and the detailed list of the references of the models may be downloaded on the EcoBase website (http://sirs.agrocampus-ouest.fr/EcoBase/).

2.4.2   Identification of the research objectives of the modeling approach

The research objectives of the 435 EwE models were classified into seven topics, i.e., (1) aquaculture; (2) ecosystem structure and functioning; (3) environmental variability and climate change; (4) fisheries; (5) marine protected areas; (6) pollution; and (7) (group of) species of

particular interest. The research objectives of each model were identified by reviewing the title, abstract and keywords of the associated publications. Note that the topics are not mutually exclusive, since a same model may have been developed to answer several questions.

Also, some of the models were used to perform specific analyses, using some of the modules or plug-ins available in the EwE software. In this study, three plug-ins of potential interest were considered: Ecotracer, EcoTroph, and Keystoneness. Ecotracer uses Ecosim to predict movement and accumulation of contaminants and tracers in food webs (Booth and Zeller, 2005; Coombs, 2004). More precisely, changes in concentrations of chemicals (e.g., persistent organic pollutants (POP) and isotope tracers) are predicted using flow rates from Ecosim along with ancillary information, such as isotope decay rate and physical exchange rates (Christensen et al., 2008). EcoTroph is based on synthetic representation of ecosystems using trophic spectra, i.e. the continuous distribution of biomass (or production, catch, fishing mortalities…) at the ecosystem scale and as a function of continuous trophic levels (Gascuel et al., 2011; Gascuel and Pauly, 2009). It enables the simulation of various fisheries changes and their impacts on computed trophic spectra, and provides indicators of the ecosystem impacts of fishing (see Chapter 3; Colléter et al., 2013a; Gasche and Gascuel, 2013; Tremblay-Boyer et al., 2011). The Keystoneness tool in the Network Analyses plug-in may be used to estimate the extent to which any functional group defined in the model functions as keystone species (Christensen et al., 2008). The methodology was implemented based on two indices of keystoneness proposed in the literature: KS#1 (Libralato et al., 2006) and KS#2 (adapted from Power et al., 1996), both based on a consensus definition of keystone species (Christensen et al., 2008).

2.4.3   Description of the complexity, structure and scales of the model

In EwE, species are aggregated into functional groups, corresponding to a single species or a group of species sharing similar ecological traits, such as size, diet, predator and life cycle (Christensen et al., 2008). The number of functional groups defined in the 435 EwE models was recorded and used as a basic descriptor of model structure. Models comprising a large number of groups have a low trophic aggregation, and thus are more complex, than models including few groups. Also, the inclusion of multi-stanza groups was considered as a supplementary descriptor of model structure. Multi-stanza groups consist of a set of groups representing different life history stages (or stanzas) that are linked together, for a species with a complex and documented trophic ontogeny. Thus, species defined using multi-stanza groups add levels of complexity in the models. Although the 435 EwE models were defined based on the implementation of the Ecopath routine, metadata indicating if the Ecosim or Ecospace routines had also been used were compiled. Ecosim and Ecospace models add complexity to the Ecopath base models.

When specified in the associated publications, the temporal and spatial scales of the 435 EwE models were collected. Typically, Ecopath models represent an average situation for a period of one year, but some models may correspond to longer time periods. Thus, records of the first and last years of the Ecopath models were compiled. The first year was used to determine the decade covered by the models, and the time period (in number of years) represented by the models was calculated. The areas (in km^2) covered by the EwE models were also documented. Lastly, currency and time units of the models were documented.

2.4.4 Characterization of the modeled ecosystems

The 435 models were classified based on the characteristics of the ecosystems they represented, using information provided in the associated publications. First, using expert knowledge, 13 ecosystem types were defined: bay/fjord, beach, channel/strait, coastal lagoon, continental shelf (down to 200 m depth), ocean (deeper than 200 m), coral reef, upwelling, estuary, lake, river, reservoir, and terrestrial. The 13 types were aggregated into three broad categories: marine (including bay/fjord, beach, channel/strait, coastal lagoon, continental shelf, coral reef, ocean, and upwelling), freshwater (comprising estuary, lake, reservoir, and river), and terrestrial.

Then, the geographic extent of the models was documented, so as to precisely locate them on the world map. To do so, a spatial shape was defined for each model, based on the coordinates or the map provided by the modelers in the associated publications (Colléter et al., 2013b). When no precise indication was given, the spatial shape was defined as a point. The centroid of the spatial shape associated to each model was used to define the climatic zone of the model. Three climatic zones were defined based on latitude: tropical-subtropical (less than 30°N/30°S), temperate (in the range 30°N-58°N/30°S-58°S), and high latitude (greater than 58°N/58°S) (Pikitch et al., 2014). The spatial shape was also used to classify the models representing marine ecosystems by FAO area and Large Marine Ecosystem (LME). FAO areas correspond to the 19 major marine fishing areas internationally established for statistical purposes by the Food and Agriculture Organization of the United Nations (www.fao.org/fishery/cwp/handbook/h/en), while LMEs correspond to 66 well-defined marine areas, usually of 200,000 km² or more, adjacent to the continents (www.lme.noaa.gov/). Therefore, only the 367 models representing marine ecosystems were classified into FAO areas,

while the subset of 347 models representing coastal marine ecosystems were classified into LMEs.

2.5   Results

2.5.1   General description of the EwE applications published worldwide

EwE models were used to tackle a wide range of ecological issues (Figure 2.1a). 87% of the models were developed to answer questions regarding the functioning of the ecosystem, 64% to analyze fisheries, 34% to focus on particular species of interest, and 11% to consider environmental variability. Less than 10% of the models looked at issues related to MPA, pollution or aquaculture. The Keystoneness module has been used in 11% of the models (47 models), whereas the EcoTroph and Ecotracer plug-ins have been rarely applied (i.e., in 2% and less than 1% of the models, respectively).

About three fourths of the 435 EwE models comprise between 10 and 40 functional groups, with 32% (141 models) including 10 to 20 groups (Figure 2.1c). Overall, the numbers of groups range from 7 to 171 groups, but only 5 models include between 75 and 100 groups, and 2 models more than 100 groups. Besides, 31% of the models comprise groups corresponding to stanzas. Time dynamic (Ecosim) versions were developed for 41% of the models, and spatially-explicit (Ecospace) versions for 7% of the models.
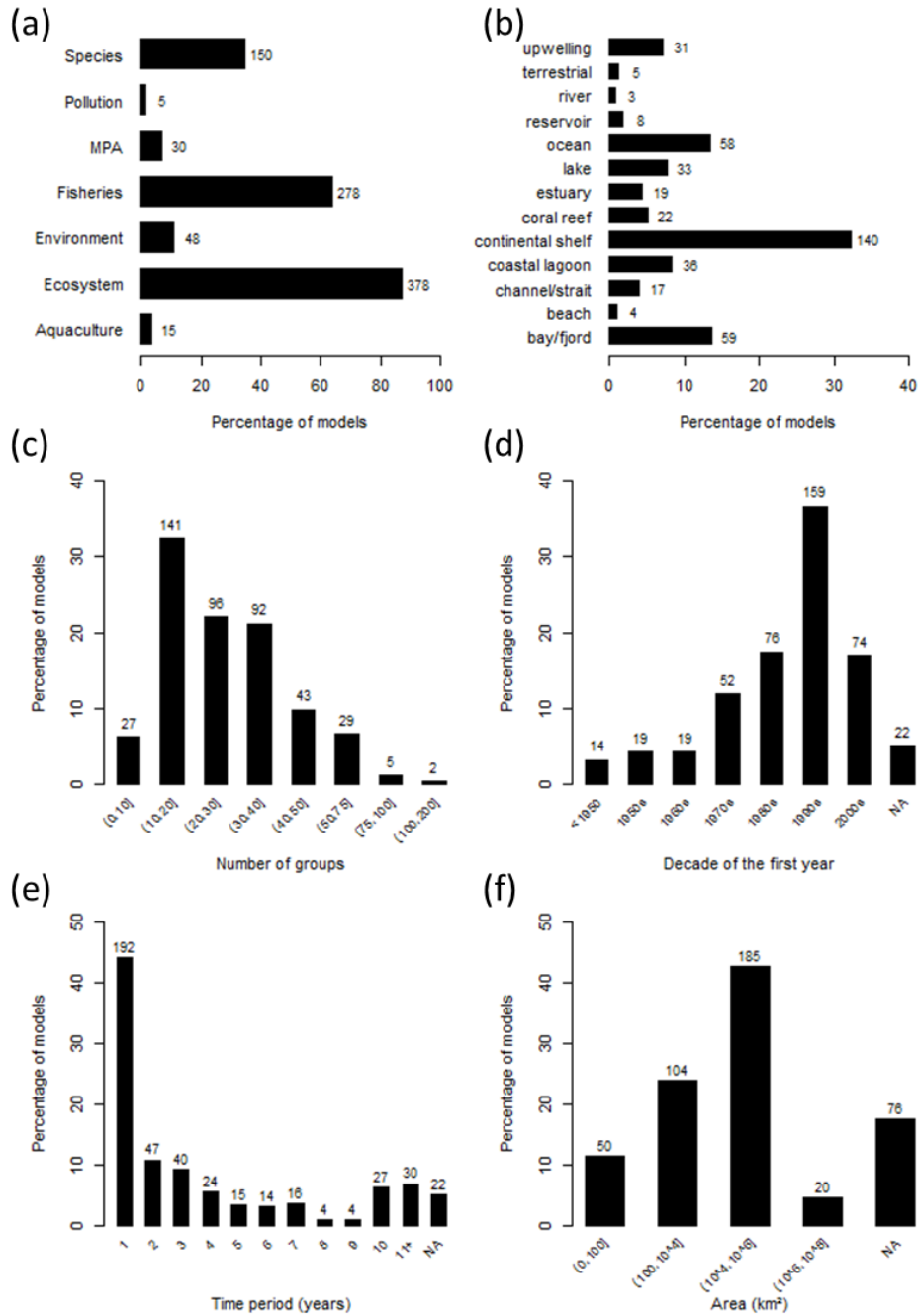
Figure 2.1 Classification of the 435 unique EwE models documented in EcoBase by: (a) research topics; (b) type of ecosystems; (c) number of functional groups; (d) decade of the first year of the models; (e) time period (in number of years) represented by the models; and (f) area (in km^2) covered by the models. On each graph, values are displayed in percentage on the y-axis and in number on the top of each bar. Missing data is displayed as 'NA' for Non Available.

About 70% of the models refer to a time period comprised between 1980 and 2009, with 37% (159 models) corresponding to the 1990s (Figure 2.1d). Besides, about three fourths of the models represent a time period lasting from one to five years, with 44% (192 models) corresponding to one year, which is the classical temporal scale of Ecopath models (Figure 2.1e). The longest time period represented by a model is 40 years. Furthermore, of the 435 unique models, about 31% (133 models) correspond to replicates of the same ecosystems. In particular, models developed to represent periods before 1950 are almost all (93%) replicates of models representing more recent periods. The spatial extent covered by the models varies widely, from 0.005 km^2 to 34,640,000 km^2. Though, model area does not exceed 1,000,000 km^2 for most models, and about half of the models cover an area ranging from 10,000 to 1,000,000 km^2 (Figure 2.1f). Twenty-two models were developed without specifying any temporal scale, and 76 models without indicating any spatial scale. 89% of the 435 EwE models use wet weight as currency unit (of which 88% express it in t·km^{-2}), 5% carbon, and 4% dry weight. Only three models use calories, one joule, and one nitrogen. Almost all models use year as time unit, while only ten models use day, month, or season.

Among the 13 ecosystem types we defined, the most represented ones in the marine category are: continental shelf (32% of the models), bay/fjord (14%), and ocean (13%) (Figure 2.1b). In the freshwater category, lake is the top represented ecosystem type, with 8% of the models. Based on the defined climatic zones, 49% of the models are located in the tropics, while 44% are located in temperate areas, and only 7% in high latitudes.
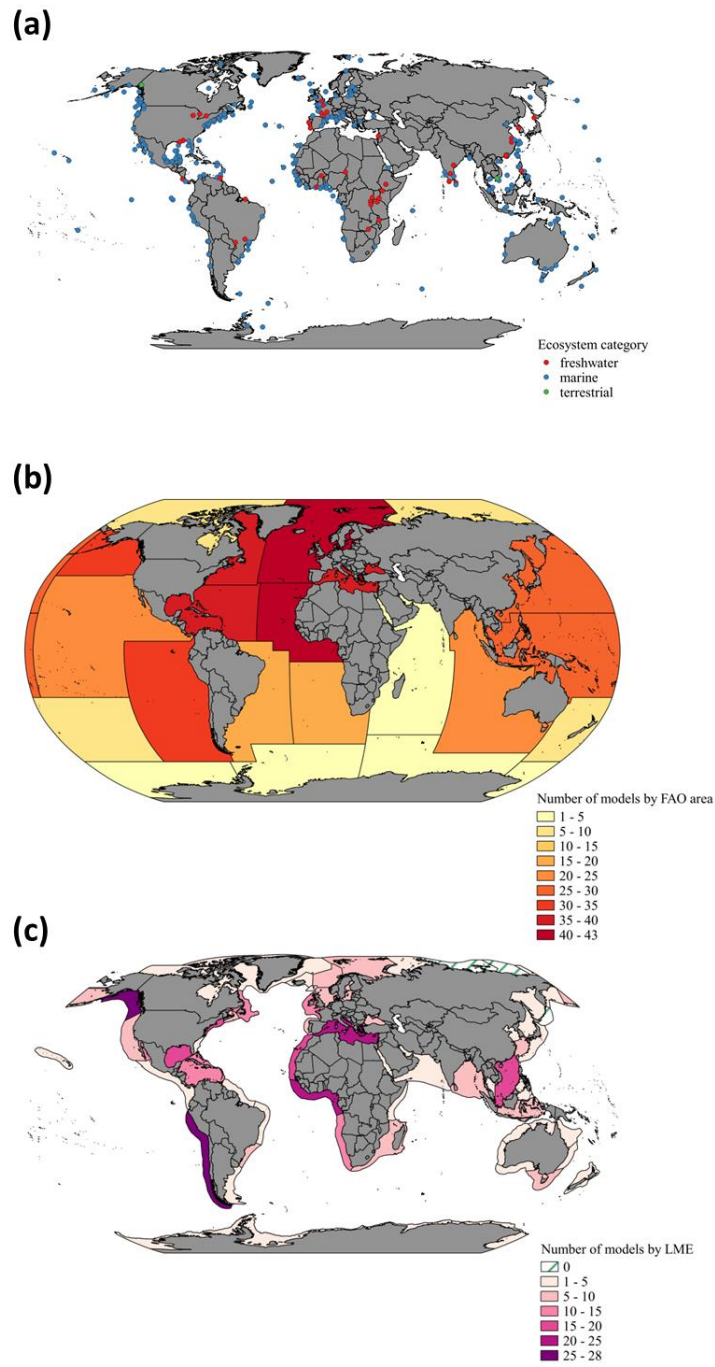
Figure 2.2 World maps of the EwE models documented in EcoBase representing (a) the centroids of the geographic extent of the models and the number of models (b) by FAO area and (c) by LME. Only the 367 models representing marine ecosystems are represented on the FAO area map, and the 347 models representing coastal marine ecosystems on the LME map.

84% of the models (i.e. 367 models) represent marine ecosystems, whereas 14% (63 models) represent freshwater ecosystems and 1% (5 models) terrestrial ones (Figure 2.2a). EwE models have been developed to study aquatic ecosystem worldwide, with some regions better covered than other. Overall, the Northern and Central Atlantic Ocean is the region with the highest proportion of EwE models (Figure 2.2b). All FAO areas comprise at least one model, but five areas concentrate about 40 models each: the Northeast Atlantic and the Eastern Central Atlantic comprise 10% of the models each; and the Western Central Atlantic, the Northwest Atlantic, and the Mediterranean and Black Sea comprise 9% of the models each. The Humboldt Current, the Gulf of Alaska, the Mediterranean and the Guinea Current are the LMEs comprising the highest number of models (at least 5% each) (Figure 2.2c). Three LMEs did not comprise any EwE models: the Oyashio Current, the East Siberian Sea, and the Laptev Sea. Overall, fewer EwE models have been developed for the Indian and Antarctic Oceans.

2.5.2 Analysis of the development of EwE applications over the past three decades

Over the past three decades, the research questions addressed using EwE models have progressively become more diversified (Figure 2.3a). Since 1984, the proportion of models developed to analyze ecosystem structure and functioning has remained the highest. However, the proportion of models looking at fisheries-related issues has significantly increased from 1984 to 2003 (from 9% in 1984-1993 to 33% in 1994-2003). The proportion of models focusing on a particular species or taxa of interest has stayed more or less constant over time (at about 15%). Although their respective proportions has remained lower than 10%, the number of models built to study environmental variability (including climate change) and MPA have gradually increased

since 1984. The numbers of models analyzing ecosystems, fisheries, or species, all show a two-fold increase between 1994-2003 and 2004-2014.

Recently developed models tend to be less aggregated and thus more complex, although highly aggregated models are still being proposed in recent times (Figure 2.3b). Indeed, during the first decade of the development of the EwE modeling approach, the total number of groups defined in the models range from 7 to 27. Over time, the range of the number of groups has expanded toward more groups, up to 67 groups in the past decade (excluding the few outlier models). Besides, the median is around 15 groups between 1984 and 1993, while it is around 30 groups between 2004 and 2014. In contrast, the time period represented by the models tends to decrease over time (Figure 2.3c). The number of years represented by the models ranges from 1 to 14 in the first decade (1984-1993), while it ranges from 1 to 8 in the last decade (2004-2014) (excluding the few outlier models). The median also shows a decrease over time, from 3 years in 1984-1993 to 1 year in 2004-2014. Moreover, the development of replicates has been increasing through time: from 24% of replicates published between 1984 and 1993, to 27% between 1994 and 2003, and 33% between 2004 and 2014. The areas covered by the models have always covered a wide range (Figure 2.3d). Nevertheless, in the past two decades, the range of the models area has expanded towards very large areas, and the median has shifted accordingly, from about 1,000 km^2 in 1984-1993 to about 100,000 km^2 in 1994-2014.
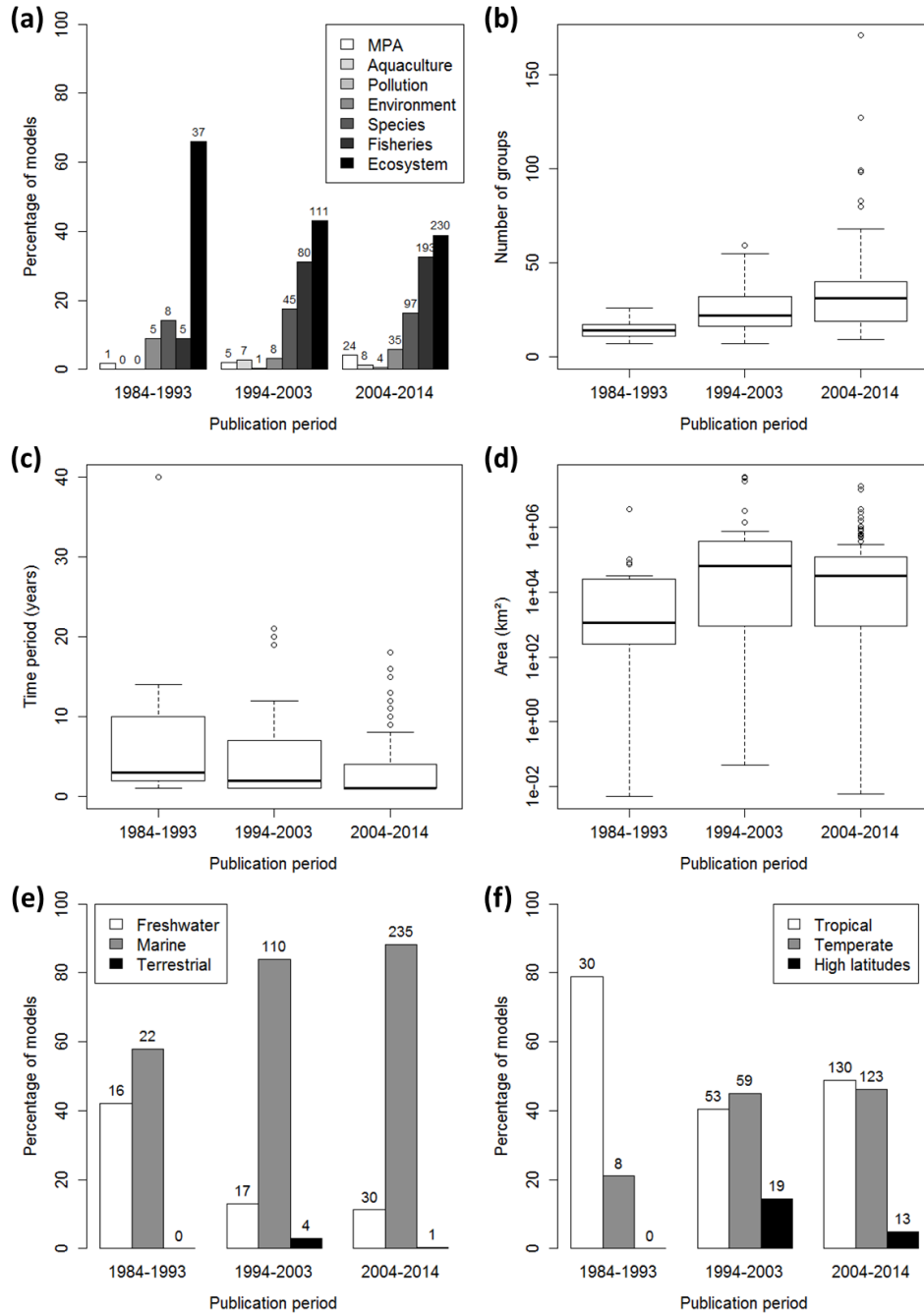
Figure 2.3 Comparison of the classified EwE models between the past three decades: 1984-1993; 1994-2003; and 2004-2014; based on the year of publication of the models. Classification of the models by: (a) research topics; (b) number of functional groups; (c) time period (in number of years) represented by the models; (d) area (in km^2) covered by the models; (e) category of ecosystem represented by the models; and (f) climatic zone of the modeled ecosystems. On each graph, values are displayed in percentage on the y-axis and in number on the top of each bar.

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The vast majority of the EwE models developed over the past thirty years represent marine ecosystems (Figure 2.3e). The numbers of models representing freshwater ecosystems has doubled over the past two decades. Nonetheless, freshwater applications represent less than 20% of the models published since 1994. Regarding climatic zones, 80% of the models represented tropical systems in the first decade (1984-1993), while the remaining 20% represent temperate systems (Figure 2.3f). Since 1994, the proportions of both tropical and temperate systems have stabilized between 40 to 50%. 32 models representing ecosystems at high latitudes have been proposed between 1994 and 2014. The same trends are observed on the maps representing the EwE models by FAO areas for each of the past three decade (Figure 2.4). From 1984 to 1993, only eight FAO areas were applied at least one model, and the Western Central Atlantic area has the highest number of models. Then, from 1994 to 2003, more models have been developed, and the Northeast Pacific and Northeast Atlantic areas show the highest number of models, while only two FAO areas located in the Antarctic do not show any model. From 2004 to 2014, all FAO areas have been applied at least one model, and the highest number of models is observed in the Eastern Central Atlantic, while the Mediterranean and Black Sea and the Northwest Atlantic areas also show a high number of models.

1984-1993

1994-2003

2004-2014

Number of models by FAO area
- 1 - 5
- 5 - 10
- 10 - 15
- 15 - 20
- 20 - 25
- 25 - 30
- 30 - 35
- 35 - 40
- 40 - 43
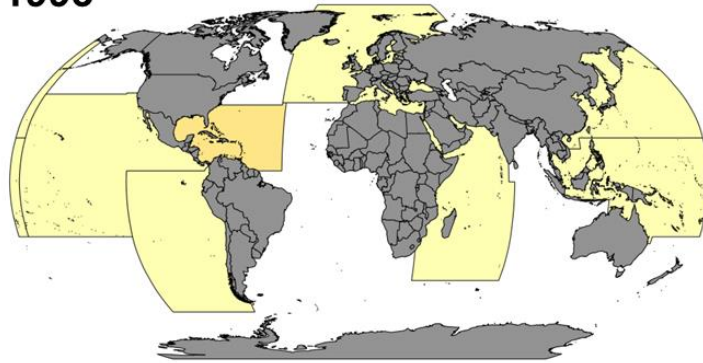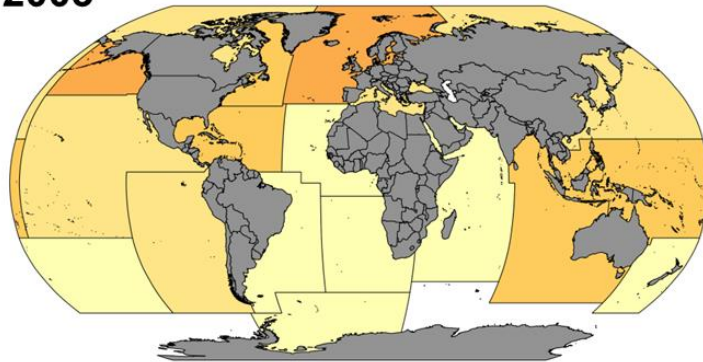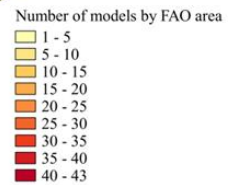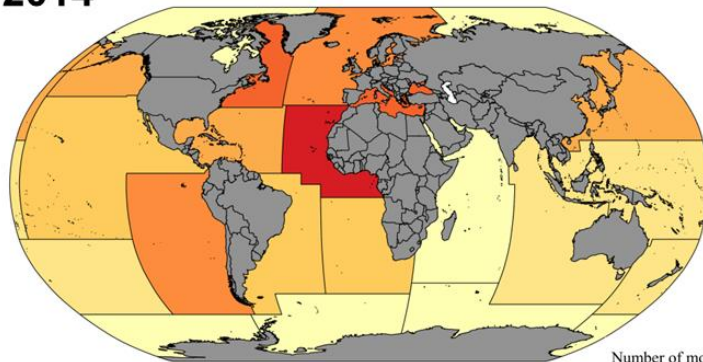
Figure 2.4 World maps of the number of EwE models by FAO areas, for each of the past three decade: 1984-1993; 1994-2003; and 2004-2014.

2.5.3 Analysis of the contribution of EwE-based studies in the scientific literature

The annual number of publications gradually increased over time (Figure 2.5). It reached a peak in 1993, increased slowly from 1994 to 2000 and more rapidly from 2000 to 2004, then stabilized at around 25 references per year. Note that the decrease observed in the annual number of publications since 2013 is not representative, due to the inventory likely being incomplete for the past two year. In fact, the Web of Science website (https://www.webofknowledge.com/) listed 46 publications having 'Ecopath' as topic in 2013, and 31 in 2014 (results obtained on the 20th of September 2014). Of the 398 EwE-based studies published over the past 30 years, 9% were published between 1984 and 1993, 29% between 1994 and 2003, and 63% between 2004 and 2014 (respectively 35, 114, and 249 publications).

The cumulated number of unique first authors significantly increased over time, from 30 researchers in 1993, to 98 in 2003, and 230 in 2014 (Figure 2.5). Both the number and proportion of research articles presenting EwE applications published in scientific journals steadily increased over the past 30 years (Figure 2.5). From 1984 to 1993, most publications corresponded to conference proceedings, mainly from the "Trophic Models of Aquatic Ecosystems" Theme session at the Statutory Meeting of ICES, in Copenhagen, in October 1990 (Christensen and Pauly, 1993b). Between 1994 and 2003, EwE-based studies were principally published as reports (with the publications of numerous *Fisheries Centre Research Reports*) or journal articles. Over the most recent period (2004-2014), publications were predominantly journal articles. Overall, 214 research articles were published in 60 different scientific journals. However, only a few of the journals published at least 4 articles. *Ecological Modeling* published the highest number of EwE-based studies (77 articles, i.e. 36%), followed by *Estuarine, Coastal and Shelf Science* (6%), and *Progress in Oceanography* (5%).
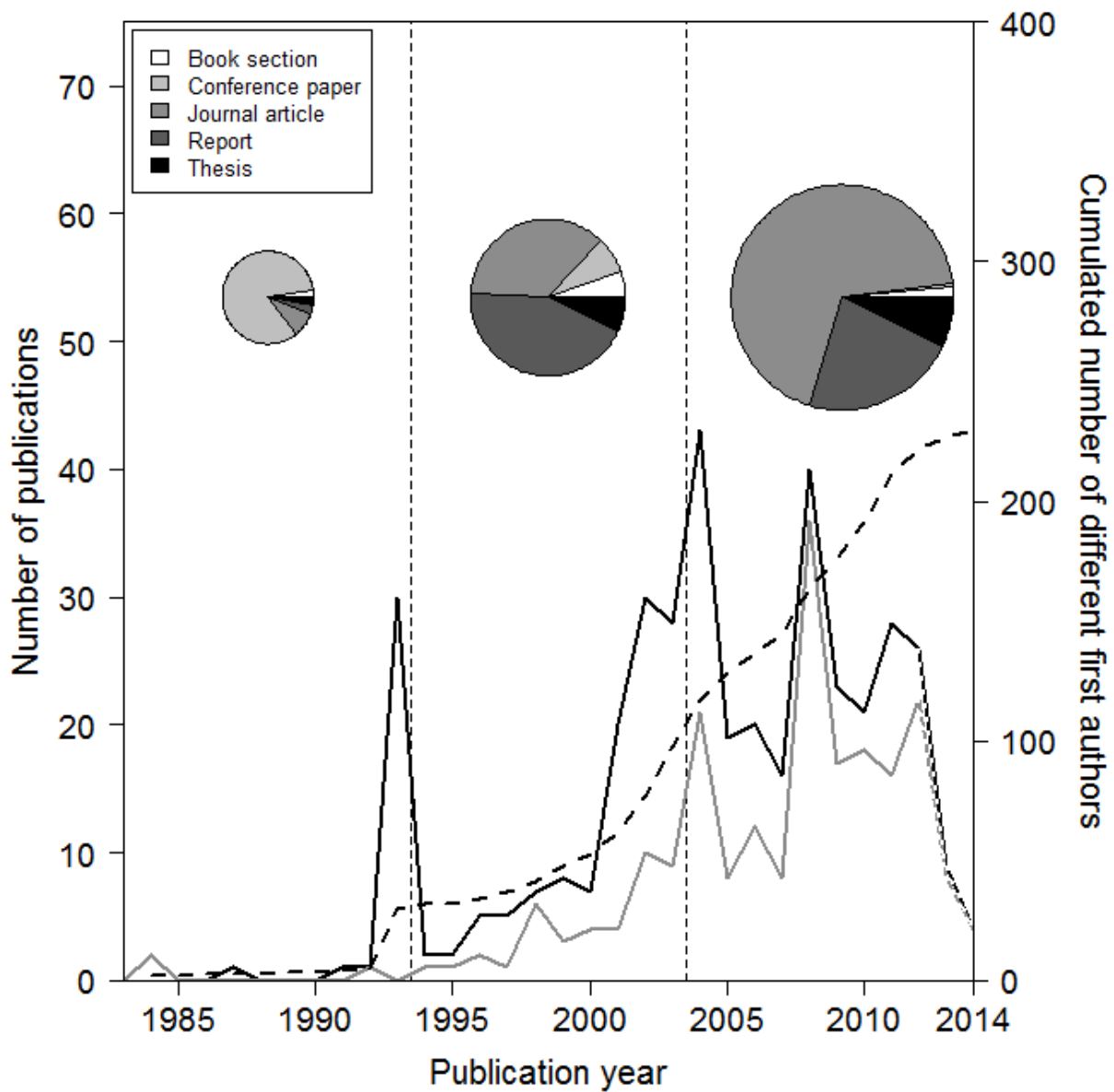
Figure 2.5 Number of publications presenting EwE-based studies over the past thirty years. For each decade (1984-1993, 1994-2003, and 2004-2014), a pie chart shows the repartition of the publications by type. The black line represents the number of all types of scientific publications while the gray line represents journal articles only. The dotted line represents the cumulated number of first authors associated to the publications from 1984 to 2014.

2.6   Discussion

2.6.1   Conclusions on the applications and evolution of the EwE modeling approach

The metadata compiled for this chapter were first used to give a global overview of the EwE applications. Overall, most models represented marine ecosystems, between 1980 and 2009, over a time period of one year, and an area ranging from 10,000 to 1,000,000 km^2. The models generally include between 10 and 40 functional groups. Most models were built to analyze ecosystem functioning and inform fisheries management, principally in ecosystems located in the Northern and Central Atlantic Ocean. Half of the models were applied to tropical systems, while more than a third of the models were used to perform time dynamic simulations in Ecosim. The Keystoneness tool is one of the most frequently applied plug-in in EwE models. Despite its complementarity with Ecopath, the EcoTroph plug-in has been applied to a few models only. In fact, Ecotroph still is a relatively recent approach, and the new development of the plug-in in R (Appendix B) may allow for a wider application (Colléter et al., 2013a).

Then, the evolution of the EwE applications over time was analyzed based on the year of publication of the models. Over the past 30 years, the numbers of both publications and modelers have steadily increased, while the proportion of journal articles presenting EwE-based studies has been growing. During the first decade of its development (1984-1993), the EwE modeling approach essentially consisted of Ecopath models representing tropical marine systems, with a simple trophic structure. The initial emphasis on the tropics was due to the development of EwE initially being centered at the International Center for Living Aquatic Resources Management (ICLARM, now WorldFish), which was based in the Philippines, and which was focused on developing methodologies for managing tropical ecosystems. In contrast, during the last two

decades (1994-2014), EwE models were applied to a wider variety of ecosystems, including polar regions and terrestrial systems, and used to analyze a wider range of research topics, including pollution, aquaculture and MPAs. The modeling practices have evolved over the past thirty years towards Ecopath models with larger spatial scales (up to 1,000,000 km^2), shorter temporal scales (typically 1 year for Ecopath), and more complex trophic structure (up to 70 functional groups). Furthermore, the proportion of models corresponding to replicates of the same ecosystem over different (anterior or posterior) time periods has been growing since 1984, up to about one third in 2004-2014. Despite the development of the Ecosim routine allowing for time-dynamic simulations, the static Ecopath routine has thus been also used to analyze changes in ecosystems over time. Indeed, using replicates of Ecopath models may constitute an easier and complementary approach to performing simulations in Ecosim, which are more complex and data-demanding. However, Ecosim has been used in a great proportion of the EwE models (41%). Despite its complementarity with Ecosim, the Ecospace routine has been little used to date (7%). This was quite surprising considering new insights Ecospace provided (Christensen and Walters, 2004), and research will be needed to expand the use of this modeling tool.

2.6.2   Challenges in the compilation and meta-analysis of EwE models

Most of the metadata analyzed in this chapter were collected from the publications presenting the models. However, detailed information was sometimes missing for many models. For instance, 5% of missing data were obtained regarding the time period represented by the models, and 17% for the area covered by the models. Though, it seems critical to clearly define and indicate the temporal and spatial scales when developing a model. Several metadata describing the physical characteristics of the modeled ecosystems were considered in EcoBase

(e.g., temperature, depth, salinity, oxygen, primary production; Colléter et al., 2013b), but information on abiotic conditions was lacking for most models.

For some metadata, the proportion of models with non-available data was too high for the outcomes to be representative, which prevented the use of the whole collection of compiled metadata in this chapter. This was notably the case with the version of the model used by the modeler. Since the EwE software evolved with time and upgraded versions were successively released, the analysis of the evolution of the use of the different versions was of potential interest. The first version of EwE, ECOPATH, was used only in the early 1980s (Polovina, 1984), and the development of a user-friendly software in the early 1990s (version 2) rapidly led to a broader use of the model. Versions 3 and 4 only had limited use, in contrast to version 5, which rapidly replaced the earlier versions, and is now itself replaced by version 6. However, versions were only specified by modelers for half of the models, so that this aspect of the modeling approach was not explored much further.

Finally, the compilation of the metadata was sometimes challenging due to some ambiguity in the description of the model. For instance, some models included functional groups labeled as stanzas, but not always properly defined as multi-stanzas groups. Thus, it was not possible to analyze in details the usage of multi-stanzas groups in EwE. The location of some models was sometimes poorly described, so that no spatial shape could be defined for these models. Information on minimum and maximum depths of the area covered by the models was critical to determine the type of ecosystem represented by the models, and was described in more or less details depending on the models.

2.6.3 Insights and perspectives from a global analysis of EwE applications

The standardized metadata provided in EcoBase will be valuable to perform meta-analyses based on EwE models. Indeed, the metadata may be used as selection criteria. By applying a scoring method on these criteria, a list of models of potential interest may be obtained. The pool of selected models may then be reused in EwE-based meta-analyses. Besides, a few recommendations for best modeling practices may be drawn from this analysis. Indeed, the metadata presented in this chapter may serve as a template of the required information which should be systematically provided when publishing EwE models. Lastly, the global and synthesized overview provided here may help to better understand the usage of and interest for the EwE modeling approach. Some regions and types of ecosystems have been widely analyzed using the EwE modeling approach, while others have remained poorly-studied. Notably, modeling effort could be concentrated in the Indian and Antarctic Oceans, seeing the small number of applications in these regions.

The current version of EwE (version 6.4) includes a large number of additional plug-ins and modules enabling various analyses, based on a static or dynamic model. It can be used to represent either marine, freshwater, or terrestrial ecosystems to answer a wide range of research questions. Thus, the number of scientific publications based on EwE models has been increasing through time, and the future integration of the most recently published EwE models might show new applications and usages of the EwE approach. Future possible developments to directly link the EwE software to EcoBase are under consideration (Appendix A), as they would help documenting more models and recording more metadata in the repository. Open-access has to become the way of thinking in ecology and the EcoBase repository was built with this idea in mind. This chapter was a first step towards a global integration of EwE-based metadata, and

more meta-analyses should be proposed in the future, thanks to the improvement of EcoBase. This is notably the case of Chapter 5 presenting a meta-analysis of marine ecosystems' trophic functioning.

Chapter 3: EcoTroph development, impacts of trophic controls on aquatic ecosystem trophic networks and fishing effects

3.1 Summary

Food web dynamics consist of processes that affect ecosystem structure and functioning. Ecosystem models are useful tools to study these aspects. Here, the EcoTroph ecosystem model is used to investigate impacts of two trophic controls (i.e., foraging arena and top-down controls) on marine ecosystem trophic flows and fishing impacts. First, the core principles and equations of EcoTroph are presented. Then, a new version of the model accounting for the foraging arena theory is developed. Cross impacts of the two trophic controls and different fishing scenarios are analyzed using a virtual ecosystem. Results showed that foraging arena controls decreased the resistance and the production of an ecosystem facing increasing fishing mortality. In contrast, the inclusion of top-down controls resulted in a more resistant ecosystem with a decrease in the kinetic of trophic flows at lower trophic levels when the abundance of higher trophic levels is reduced by fishing. These two controls increased the interactions between TLs, and, in part, shaped fishing impacts at the ecosystem scale. Then, ET was applied to three real ecosystems which have been previously modeled using Ecopath with Ecosim. EcoTroph and Ecosim predictions related to changes in fishing effort were compared, and showed that accounting for trophic controls enabled EcoTroph to mimic Ecosim models, and better reflect associated changes in trophic flows. The three case studies exhibited different behaviors: while the pelagic ecosystem had strong foraging arena controls but no top-down controls, the mixed ecosystems were characterized by weaker foraging arena controls but effective top-down controls. This

enabled to finally discuss realism and parameterization of ecosystem models to predict fishing impacts on whole ecosystems.

3.2   Introduction

It is important to improve our understanding of predator-prey interactions and impacts of fishing beyond targeted species. However, understanding and predicting consequences of altered trophic interactions is an arduous task (McCann, 2007). A great number of food web modeling approaches have been developed (Whipple et al., 2000); and several ecosystem models, such as Ecopath with Ecosim (Christensen and Pauly, 1992; Christensen and Walters, 2004), OSMOSE (Shin and Cury, 2004, 2001), Atlantis (Fulton et al., 2011), or EcoTroph (Gascuel et al., 2011; Gascuel and Pauly, 2009), have been applied to an increasing number of marine ecosystems. Each model type is based on different assumptions and hypotheses, and represents only one of many possible visions of an ecosystem. Ecosim is based on the 'foraging arena theory' (see Section 3.4.1), in which it is assumed that spatial and temporal restrictions in predator and prey activity cause partitioning of each prey population into vulnerable and invulnerable components (Ahrens et al., 2012; Walters et al., 1997; Walters and Juanes, 1993; Walters and Korman, 1999). Foraging arenas appear common and cover a wide variety of mechanisms in aquatic systems, notably restrictions of distributions in response to predation risk, and risk-sensitive foraging behavior (review in Ahrens et al., 2012). The principles of foraging arena theory have been widely used, mainly through the application of Ecosim, to explain and model historical fishing impacts on whole ecosystems (review in Walters and Martell, 2004). Several predictions have been made possible to better understand the functioning of trophic networks at different scales,

notably that trophic cascades should be common at least in simpler aquatic ecosystems, and surplus production should occur for predators in harvested systems (Ahrens et al., 2012).

The models needed for EAF practitioners should have the capability of accounting for trophic controls to enhance analyses and predictions of fishing impacts. As a contribution to such effort, a major improvement to EcoTroph is presented in this chapter. EcoTroph is a recently developed approach and software for modeling aquatic ecosystems, articulated entirely around the trophic level concept. The EcoTroph model constitutes a useful tool to study impact of ecological processes on ecosystem trophic flows and fishing impacts through a simple framework. Firstly, its current formulation is presented (Section 3.3). However, this formulation does not account for behaviors typically predicted by foraging arena theory. Thus, a new ET formulation accounting for foraging arena consumption rate limitations was developed (Section 3.4), i.e., an approach to represent how the biomass flow through a TL class that has been reduced by fishing may be limited by the very biomass in that TL class. Cross impacts of ecosystem trophic properties (top-down and foraging arena controls) and fishing impacts were analyzed on a virtual ecosystem. Changes in trophic flows and resistance, two key aspects that could be impacted by these trophic properties, were assessed. Finally, ET was applied to three real ecosystems which have been previously modeled using Ecopath with Ecosim. EcoTroph and Ecosim predictions were compared considering historical fishing effort changes and different EcoTroph parameterizations. Three EwE models were selected: one EwE model representing a predominantly pelagic ecosystem, the central North Pacific Ocean (Cox et al., 2002a, 2002b), and two models representing different mixed ecosystems, the Gulf of Thailand (FAO/FISHCODE, 2001) in the South China Sea; and the Guinean continental shelf (Gascuel et al., 2009a). Patterns associated with foraging arena parameterization were supposed to be

different considering differences in predator-prey relations in these ecosystem types. This enabled us to discuss theoretical and applied results of foraging arena and top-down controls on ecosystem trophic flows and fishing impacts, but also realism and parameterization of ecosystem models to predict fishing impacts on whole ecosystems.

3.3 The EcoTroph model and its use

3.3.1 EcoTroph core principles and equations

TLs characterize the position of organisms within trophic networks (see Section 2.3). They may change during ontogeny (Pauly et al., 2001), and vary in time and space as the function of encountered prey organisms. However, for any ecosystem state, the TL of each organism or the mean TL of each species results from the ecosystem trophic functioning. Therefore, TL appears as a state variable characterizing each unit of biomass.

EcoTroph is an ecosystem approach based on two key ideas. The first key idea is that an ecosystem can be represented by the distribution of its biomass across trophic levels (TLs). This distribution is called the biomass trophic spectrum (Gascuel et al., 2005). The biomass enters the food web at TL=1, as generated by the photosynthetic activity of primary producers and recycling by the microbial loop (Figure 3.1). Between TL=1 and TL=2, the biomass is composed of mixotrophs only, i.e., of organisms that are simultaneously primary producers and first-order consumers, such as e.g., giant clams. Their biomass is usually low, and is conventionally split between biomasses at TL=1 and 2. Then, at TLs>2, the biomass is composed by heterotrophic organisms with mixed diet and fractional TLs resulting in a continuous distribution of biomass along TLs.
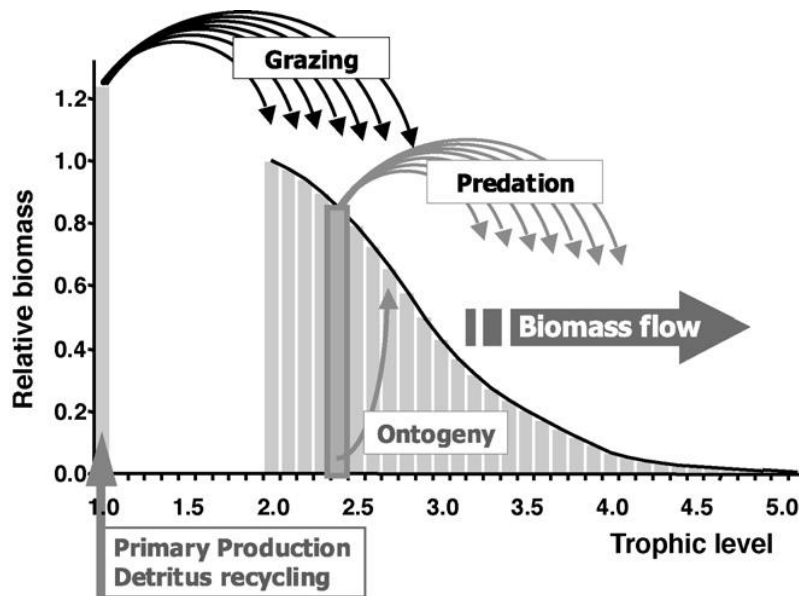
Figure 3.1 Diagram of the trophic functioning of an ecosystem according to the EcoTroph model. Theoretical distribution of the biomass by trophic level and trophic transfer processes, given an arbitrary input of biomass (fixed equal to 1 for TL=2) (adapted from Gascuel and Pauly, 2009).

The second key idea is that the trophic functioning of marine ecosystems is modeled as a biomass flow surging up the food web from lower to higher trophic levels (Figure 3.1). Each organic particle moves more or less rapidly up the food web according to abrupt jumps caused by predation and to continuous processes (ontogenic changes in TLs). All particles jointly constitute a biomass flow modeled as a continuous model (Gascuel et al., 2008). Based on the traditional equations of fluid dynamics, the biomass flow $\Phi(t,\tau)$, i.e., the quantity of biomass moving up through TL τ at every moment t, is expressed as:

$$\Phi(t,\tau) = D(t,\tau) \times K(t,\tau) \tag{3.1}$$

where $\Phi(t,\tau)$ is expressed in t.year^{-1}, $D(t,\tau)$ is the density of biomass at TL τ (expressed in t.TL^{-1}), and $K(t,\tau)=d\tau/dt$ is the flow kinetic, which quantifies the velocity of biomass transfers in the food web (expressed in term of the number of TLs crossed per year, i.e., in TL.year^{-1}). Under steady-state conditions, Eq. (3.1) becomes:

$$D(\tau) = \frac{\Phi(\tau)}{K(\tau)} \qquad (3.2)$$

A discrete approximation of the continuous distribution $D(\tau)$ is used for mathematical simplification and visual representation (see Figure 3.1). Thus, the continuous distribution of the biomass across TLs is approximated using narrow classes $[\tau, \tau+\Delta\tau[$. As a convention (and based on previous studies; Gascuel et al., 2011; Gascuel and Pauly, 2009), trophic classes of width $\Delta\tau=0.1$ TL were considered to be an appropriate resolution, and a range starting at TL=2 (corresponding to the first-order consumers), up to TL=5.5 (with calculations performed up to TL=7), an appropriate range to cover all top predators likely to occur in marine systems (Cortés, 1999; Pauly et al., 1998). Therefore, mean values D_τ, Φ_τ, and K_τ over the trophic class $[\tau, \tau+\Delta\tau[$ are considered. Thus, Eq. (3.2) becomes:

$$D_\tau = \frac{\Phi_\tau}{K_\tau} \qquad (3.3)$$

Under steady-state conditions, the biomass (in tonnes) present at any moment within the trophic class $[\tau, \tau+\Delta\tau[$ is:

$$B_\tau = \int_\tau^{\tau+\Delta\tau} D(\tau) \times d\tau = D_\tau \times \Delta\tau \qquad (3.4)$$

So, according to Eq. (3.3), the biomass B_τ is expressed as:

$$B_\tau = \frac{\Phi_\tau}{K_\tau} \times \Delta\tau \qquad (3.5)$$

Moreover, the biomass flow $\Phi(\tau)$ is a density of production at TL τ. Therefore, the production of a trophic class $[\tau, \tau+\Delta\tau[$ is:

$$P_\tau = \int_\tau^{\tau+\Delta\tau} \Phi(\tau) \times d\tau = \Phi_\tau \times \Delta\tau \qquad (3.6)$$

Production is commonly expressed in t.year^{-1}. In fact, it implicitly refers to the conversion of biomass eaten at TL τ-1, into predator tissues whose mean TL is τ. Therefore, in a TL-based approach such as EcoTroph, production has to be expressed in t.TL.year^{-1}, i.e. tonnes moving up the food web by 1 TL on average during 1 year. This ensures consistency in the units used.

As natural losses occur during trophic transfers (through non-predation mortality, respiration, and excretion), the biomass flow Φ_τ is a decreasing function of TL. Biomass removal by fisheries can be considered as an additional diversion of one part of the trophic flow that bolsters this negative natural trend. Therefore, from one trophic class to the next, the biomass flow is calculated as:

$$\Phi_{\tau+\Delta\tau} = \Phi_\tau \times exp(-(\mu_\tau + \varphi_\tau) \times \Delta\tau) \qquad (3.7)$$

where μ_τ and φ_τ (expressed in TL^{-1}) are, respectively, the mean rate of natural loss and the mean loss rate attributable to fishing over a $[\tau, \tau+\Delta\tau[$ interval. Eq. (3.7) implies that the biomass flow at a given TL depends on the flow from lower TLs. In other words, it implicitly introduces a bottom–up control of prey on predators in the model. Eq. (3.7) also defines the net transfer efficiency (NTE) between continuous TLs as exp(-μ_τ).

The speed of the biomass flow K_τ (flow kinetic) depends on the turnover of the biomass, and is defined using mean values per trophic class. It is deduced from Eqs. (3.5) and (3.6):

$$K_\tau = \left(\frac{P}{B}\right)_\tau \qquad (3.8)$$

Under equilibrium assumption, Allen (1971) demonstrated that P/B=Z, with Z the total mortality. Here too, the production implicitly refers to one TL jump in the food web, and unit consistency requires rewriting Allen's equation as:

$$\frac{1}{\Delta\tau = 1}\left(\frac{P}{B}\right) = Z, \text{ and hence } K_\tau = (F_\tau + M_\tau) \tag{3.9}$$

Where the term ($\Delta\tau$=1), useful only for unit consistency, is omitted, and where F_τ and M_τ are respectively the usual fishing and natural mortalities (in year^{-1}).

Starting from a reference state, Eq. (3.7) may be used to simulate the biomass flow for various fishing patterns defined by their fishing loss rates φ_τ. Predation being an important source of mortality, a top-down control effect is introduced into the model assuming that a fraction α_τ of the natural mortality M_τ depends on predator abundance as follows:

$$M_\tau = \alpha_\tau \times M_{ref,\tau} \times \left(\frac{B_{pred}}{B_{ref,pred}}\right)^\gamma + (1 - \alpha_\tau) \times M_{ref,\tau} \tag{3.10}$$

where the subscript 'ref' indicates the reference state and B_{pred} is the biomass of predators (conventionally equal to the biomass of the [τ+0.8, τ+1.3[trophic class; Gascuel et al., 2009b). The coefficient α_τ, i.e., the top-down coefficient varies between 0 and 1 and determines the part of natural mortality at TL τ dependent on predator abundance. The coefficient γ is a shape parameter varying between 0 and 1 and defines the functional relationship between prey and predators. A value of 1 results in a linear effect of the abundance of predators on the flow kinetics; a smaller value would turn the equation into a non-linear relationship akin to Holling's type II. The top-down equation is deduced from Eqs. (3.9) and (3.10):

$$K_\tau = (K_{ref,\tau} - F_{ref,\tau}) \times \left[1 + \alpha_\tau \times \left(\frac{B_{pred}^\gamma - B_{ref,pred}^\gamma}{B_{ref,pred}^\gamma}\right)\right] + F_\tau \tag{3.11}$$

Starting with the reference state of the ecosystem, where the flow kinetics $K_{ref,\tau}$ is known (see Section 3.3.2), Eq. (3.11) enables to simulate K_τ for various changes in the fishing patterns, and to account for indirect impacts of fishing on the ecosystem when performing simulations. Fishing, reducing the life expectancy of targeted species, can be the cause of notable accelerations in ecosystem's flow kinetics. Note that Equation (3.11) requires an estimate of predator biomass, which is based on Eq. (3.5). As this last equation reciprocally includes flow speed, the solution must involve an iterative procedure, starting with the reference values of K_{ref} estimating K for a given F, then estimating B, and iterating until K and B estimates stabilize.

Additionally, the current version of ET (Gasche and Gascuel, 2013; Gascuel et al., 2011) is based on two distinct compartments, one accounting for the whole ecosystem biomass and one solely for the biomass accessible to fisheries. The same equations (Eqs. (3.5), (3.7), and (3.11)) are used for both compartments, but their parameters differ since they take into account the fact that exploited species usually do not have the same characteristics as the unexploited ones. Parameters of the accessible part of the biomass are noted B_τ^*, Φ_τ^*, K_τ^*, or F_τ^*. Thus, a selectivity coefficient S_τ is defined as the fraction of the ecosystem biomass accessible to fisheries. It can be estimated in the reference state ($S_{ref,\tau} = B_{ref,\tau}^*/B_{ref,\tau}$), based on field observations or from a theoretical model (see Section 3.3.2). These parameters allow simulation of the accessible biomass flow for any value of the accessible fishing loss rate φ_τ^*. The computations are initialized for secondary producers (if no fishing at TL=1, otherwise initialized at TL=1) by:

$$\Phi_2^* = \Phi_{ref,2}^* \times \frac{\Phi_2}{\Phi_{ref,2}} = \Phi_2 \times S_{ref,2}$$

And then

$$\Phi_{\tau+\Delta\tau}^* = \Phi_\tau^* \times exp[-(\mu_\tau^* + \varphi_\tau^*) \times \Delta\tau] \qquad (3.12)$$

The accessible biomass is simulated from:

$$B_\tau^* = \frac{\Phi_\tau^*}{K_\tau^*} \times \Delta\tau \qquad (3.13)$$

where K_τ^* is the kinetic of the accessible flow, deduced from the reference state $K_{ref,\tau}^*$ (see Section 3.3.2) based on Eq. (3.11).

Finally, catches per time unit (in t.year^{-1}) are derived from earlier equations. They can be expressed either as the integration over time of instantaneous catches dY/dt, or as the integration over TLs of the catch densities dY/dτ, leading to:

$$Y_\tau = \int_{t=0}^1 \frac{\varphi_\tau^*}{\varphi_\tau^* + \mu_\tau^*} \times [\Phi^*(\tau) - \Phi^*(\tau + \Delta\tau)] \times dt \qquad (3.14)$$

or

$$Y_\tau = \int_{s=0}^{\Delta\tau} \varphi_\tau^* \times \Phi^*(\tau + s) \times ds \qquad (3.15)$$

Eq. (3.14) indicates that catches are equal to the fraction of flow loss attributable to the fishery, whereas Eq. (3.15) stems from the definition of the fishing loss rate. Integration of Eqs. (3.14) or (3.15) both lead to the catch equation, which can be expressed, after simplification as:

$$Y_\tau = \varphi_\tau^* \times \Phi_\tau^* \times \Delta\tau = \varphi_\tau^* \times P_\tau^*$$
$$\text{or } Y_\tau = F_\tau^* \times B_\tau^*, \text{ with: } F_\tau^* = \varphi_\tau^* \times K_\tau^* \qquad (3.16)$$

where F_τ^* is the fishing mortality of the accessible biomass, P_τ^* the production of the accessible biomass, and Y_τ is the annual catch from the [τ, τ+Δτ[trophic class. Equations presented here constitute the core of the ET-Transpose and ET-Diagnosis routines accessible through an R

package (see Section 3.3.2, and Appendix B) available on the R Cran (Colléter et al., 2013a), or an EwE plug-in (www.ecopath.org).

3.3.2 EcoTroph parameterization and use

Throughout this thesis, EcoTroph was used to analyze two kinds of ecosystems: virtual ecosystems (see Section 3.4.2), and case studies modeled using Ecopath (see Section 3.4.3, Chapter 4, and Chapter 5). As explained in Section 3.3.1, the EcoTroph model requires as input data several parameters by trophic class: two of the three parameters B_{ref}, K_{ref}, and Φ_{ref} (the remaining one is calculated using the two others), Y_{ref} the catches (or either F_{ref} or φ_{ref}), and the selectivity S. These data define the reference state, on which several simulations of changes in fishing mortality can be done.

The reference state for a virtual ecosystem usually refers to an unexploited state. It is commonly defined using an arbitrary $\Phi_{ref,1}$ and an associated net transfer efficiency to derive $\Phi_{ref,\tau}$ for each trophic class (see Section 3.4.2). The speed of the biomass flow $K_{ref,\tau}$ (flow kinetic) is estimated for each trophic class using an empirical model developed by Gascuel et al. (2008). The P/B ratio and therefore $K_{ref,\tau}$ is expressed as a function of the TL and the mean water temperature. Lastly, theoretical fishing patterns, i.e. F_τ or φ_τ, and S_τ are defined to simulate different fishing impacts (see Section 3.4.2)

The reference state for real case studies is usually derived from an Ecopath model. It is computed by converting Ecopath data referring to functional groups into data referring to trophic classes. For each Ecopath group, the biomass is distributed across TLs assuming that this distribution follows a lognormal curve, defined by the TL of the trophic group in question as a mean, and a standard deviation, which is a measure of the TL variability within the group

(conventionally defined according to an empirical model; see Appendix B). The biomass trophic spectrum is the curve obtained by summing the biomass of all functional groups across TLs. The same procedure can be applied to the catch of the functional groups or their production (calculated for each group as P=P/B*B) to create respectively a catch or production trophic spectrum. $K_{ref,\tau}$ can be derived from the production/biomass $(P/B)_\tau$ ratios of each trophic class. Since EcoTroph is based on two distinct compartments (one accounting for the whole ecosystem biomass and one solely for the biomass accessible to fisheries), simulations required setting up the accessibility to fishers of each trophic group in the Ecopath model, a parameter that has been theoretically defined as the proportion of a species or group that would be caught under the hypothesis of an infinite fishing effort (Gascuel and Pauly, 2009). This parameter takes into account whether a species is targeted by fisheries or not. Therefore a trophic group composed of a few target species and a lot of non-target species will have a lower accessibility than a group containing only targeted species (see Appendix B). This enables to calculate the parameters $B_\tau^*, \Phi_\tau^*, K_\tau^*,$ or F_τ^* related to the biomass accessible to fisheries.

Starting from these reference states, Eqs. (3.5), (3.7), and (3.11) enable the calculation of biomasses, productions, etc… at the equilibrium for each trophic class and various fishing patterns defined by their fishing loss rates φ_τ. As these equations are interrelated, the solution must involve an iterative procedure, starting with the reference values of K_{ref} and Φ_{ref}, estimating K and Φ for a given F, then estimating B, and iterating until K, Φ, and B estimates stabilize. Effects of fishery mortality changes at an ecosystem scale include biomass and kinetic changes (see Appendix B), but also impacts on the mean trophic levels of the catch and of the total biomass (Gascuel and Pauly, 2009).

Two ET routines (also available as R-functions; Appendix B) are used. ET-Transpose enables the conversion of data referring to functional groups (extracted from Ecopath) into data referring to trophic classes in order to create trophic spectra. These data represent the current distribution of biomass B_τ, production P_τ, catches Y_τ, fishing mortality F_τ ($F_\tau = Y_\tau / B_\tau$), or fishing loss rate ($\varphi_\tau = Y_\tau / P_\tau$) across TLs, as well as $B_\tau^*, P_\tau^*, Y_\tau^*, F_\tau^*$, and φ_τ^* the equivalent parameters for the accessible part of the ecosystem. ET-Diagnosis is used to simulate the effect of different fishery mortality scenarios on trophic spectra coming from ET-Transpose. Different effort multipliers are applied to the initial fishing mortalities. For instance, a null effort multiplier corresponds to a fishery closure (F=0), and allows users to rebuild an estimate of the unexploited status of the studied ecosystem.

3.4 Analysis of the impacts of trophic controls: materials and methods

3.4.1 Including foraging arena consumption rate limitations in EcoTroph

EcoTroph is based on a continuous representation of trophic flows. This differs from the EwE approach where biomass is split between various trophic boxes. However, homologies between EwE and ET help understand aspects of both models. In EwE, each box generates during each time unit a biomass production (P) at trophic level τ, of which a part Q is consumed by predators, whose production occurs on average at trophic level $\tau+1$ (Figure 3.2). Thus, the production $P(\tau+1)$ constitutes a trophic flow transferred from level τ to level $\tau+1$. Furthermore, trophic flows appear to be the consequence of two processes: predation (M_2), by which biomass is transferred from a prey to a predator, and growth, through which the predator converts the biomass of trophic level τ into its own biomass, on average at trophic level $\tau+1$. Losses occur due

to four processes during these transfers: catches (Y), non-predation mortality (M_0), excretion (U) and respiration (R, see Figure 3.2). The first of these four processes is accounted for in ET Eq. (3.7) using the fishing loss rate parameter φ_τ, which is related to fishing mortality F_τ. The three others are implicit in the natural loss rate parameter μ_τ. Thus, in both models, the ecosystem is represented as a trophic flow moving from lower to upper trophic levels, with losses due to non-predation mortality, catches, excretion and respiration.
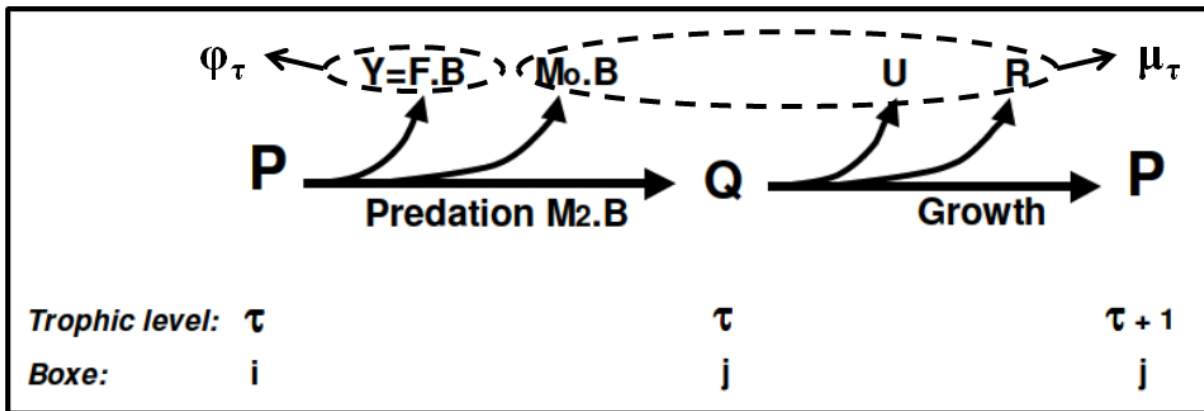
Figure 3.2 Schematic representation of the conceptualization of biomass flow in EwE: the production P of the prey i at trophic level τ is split into three parts: predation (M2.B=Q), losses due to non-predation mortality (M0.B) and fisheries catches (F.B=Y). Of the amount Q, only a small fraction is transferred by the predator j from trophic level τ to $\tau+1$, due to losses connected with excretion (U) and respiration (R). These processes are integrated into φ_τ and μ_τ EcoTroph parameters (adapted from Gascuel et al., 2009b).

However, there is a large difference between the underlying logic of these two models. The Ecosim dynamic model is based on the foraging arena theory: spatial and temporal restrictions in predator and prey activity cause partitioning of each prey pool B_{prey} as having an available component, V, and an unavailable (safe) component, $B_{prey} - V$, to each predator pool

B_{pred}, at any moment in time (Figure 3.3). Prey organisms alternate between these two components at rates v and v' (called vulnerabilities) with a flux rate: $v \times (B_{prey} - V)$ to the available one, and a flux rate: $v' \times V$ to the unavailable one. Finally, it assumes that biomass flow rate Q from prey to predator satisfies the mass-action relationship: $Q = a \times V \times B_{pred}$, with 'a' the predator rate of search for the prey pool (see Figure 3.3) (Ahrens et al., 2012; Walters et al., 1997; Walters and Juanes, 1993; Walters and Martell, 2004).
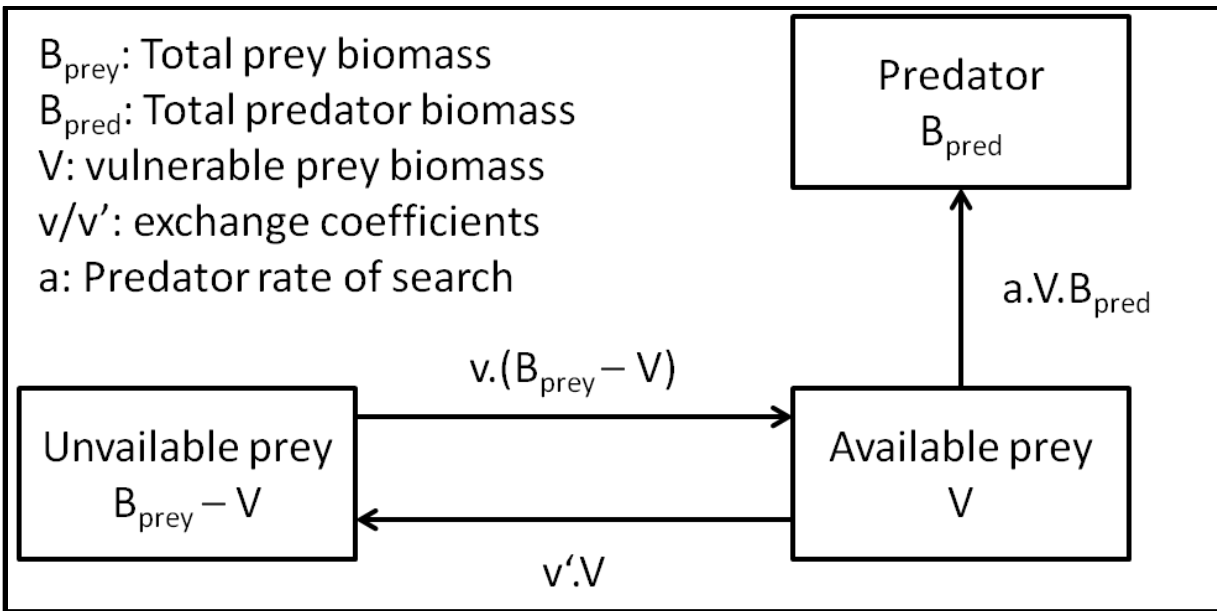
Figure 3.3 Foraging arena approach used in Ecosim to simulate dynamic change in biomass flow between the unavailable and available components of the prey pool, and the predator pool (adapted from Walters et al., 1997).

Therefore, the foraging arena model for the consumption Q recognizes that prey and predator behaviors may severely limit consumption rates:

$$Q = \frac{a \times v \times B_{prey} \times B_{pred}}{v + v' + (a \times B_{pred})} \tag{3.17}$$

Dividing Eq. (3.17) by predator biomass B_{pred} enables the calculation of the instantaneous food-intake rate of prey per predator, i.e., Q/B_{pred}. This last element can be much higher at low predator biomass than the natural rate whether or not there is any increase in prey biomass.

In contrast, ET Eq. (3.7) predicts an exponential decline in production with an increasing TL. The current formulation permits top-down control effects (Eq. (3.11)), and assumes a bottom-up loss of biomass flow due to harvesting and natural loss (Eq. (3.7)). However, Eq. (3.7) does not recognize the fact that the biomass flow, Φ_τ, may be directly limited by the prey biomass at the same trophic level τ, i.e., production is assumed to be purely 'donor controlled'. A foraging arena formulation for Eq. (3.7) was developed, representing how the biomass flow through a TL class that has been reduced by fishing may be limited by the very biomass in that TL class. In fact, the use of the foraging arena theory in models like EwE should cause the predictions of these models to diverge in a very fundamental way from EcoTroph predictions, since these models predict severe limits on compensatory increase in productivity as predator biomasses are reduced. In Eq. (3.17), Q is predicted to increase asymptotically as B_{pred} increases, toward the maximum flow rate $Q_{max} = v \times B_{prey}$ with the steepness of this increase determined by the 'a' parameter (see detailed calculations in Ahrens et al., 2012; Walters and Martell, 2004). Thus, such an asymptotic effect was included to account for foraging arena consumption rate limitations. A consumption limitation modifier H was integrated in Eq. (3.7), which modifies $\Phi_{\tau+\Delta\tau}$ using an asymptotic effect scaled relative to the reference biomass flow at trophic level $\tau+\Delta\tau$, $\Phi_{ref,\tau+\Delta\tau}$ (reference situation before simulation; see Figure 3.4):

$$\Phi_{\tau+\Delta\tau} = \Phi_\tau \times exp(-(\mu_\tau + \varphi_\tau) \times \Delta\tau) \times H(\tau + \Delta\tau) \qquad (3.18)$$

with H the consumption limitation modifier:

$$H(\tau + \Delta\tau) = \omega + (1 - \omega) \times \frac{G \times \Phi_{\tau+\Delta\tau}/\Phi_{ref,\tau+\Delta\tau}}{1 + (G - 1) \times \Phi_{\tau+\Delta\tau}/\Phi_{ref,\tau+\Delta\tau}} \qquad (3.19)$$
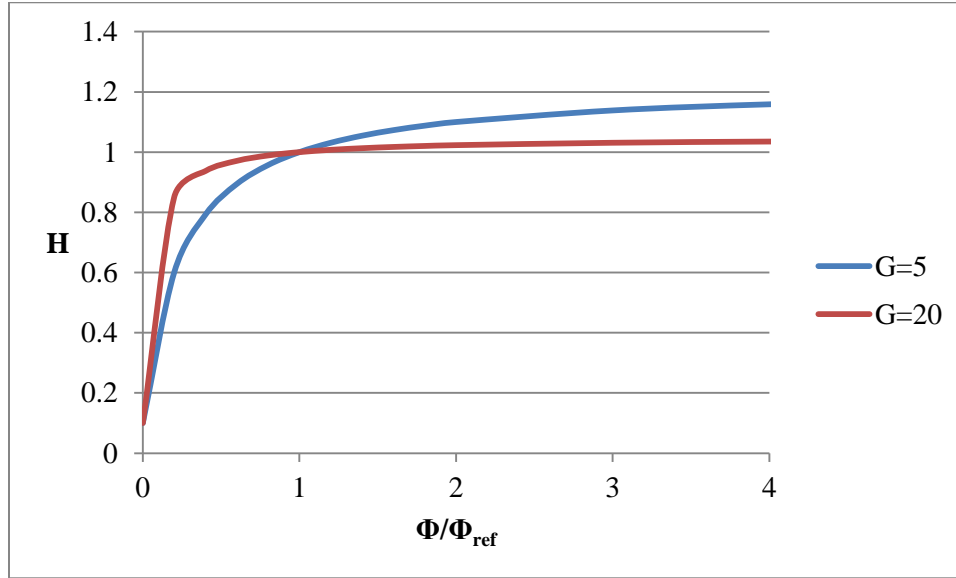
Figure 3.4 Value of the H modifier as a function of the ratio Φ/Φ_{ref} for G=5 and 20.

Eq. (3.19) assumes that a proportion ω of the biomass flow is due to ontogenetic changes in feeding, and the remaining proportion is dependent on the relative biomass flow rate $\Phi_{\tau+\Delta\tau}/\Phi_{ref,\tau+\Delta\tau}$. The Goodyear compensation ratio G, parameter coming from the analysis of recruits vs. spawning stock biomass (see Walters et al., 2008), is a good proxy for the biomass compensation ratio (see Appendix C; Ahrens et al., 2012; Walters et al., 1997). Ecosim models typically predict G values of at least 2, and commonly greater than 10 (Walters et al., 2008; Walters and Martell, 2004). Eq. (3.18) was implemented in EcoTroph equations, and impacts on trophic flows and fishing effect of the top-down control (α parameter, Eq. (3.11)), and the foraging arena consumption limitation modifier (ω and G parameters, Eq. (3.19)) were analyzed.

3.4.2 Application of EcoTroph to a virtual ecosystem

In this chapter, EcoTroph was first used to simulate a virtual ecosystem facing various exploitation patterns. The virtual ecosystem used as reference state was unexploited ($\varphi_{ref,\tau}=0$), and had the following characteristics:

- Biomass flow: the value of primary production, $\Phi_{ref,1}$, was set at 1000 arbitrary units, such that the biomass flow of the first trophic class considered in the model ($\Phi_{ref,2}$) was equal to 100 using a standard NTE of 10% (see below);

- Net transfer efficiency: a unique standard value of $\exp(-\mu_\tau)=0.10$ was used for all trophic levels (Pauly and Christensen, 1995);

- Flow kinetics: standard flow kinetics were considered, based on empirical equations by Gascuel et al. (2008), for a mean water temperature of 15°C.

Impacts on biomass of increasing fishing efforts were simulated based on several selectivity curves that defined the part of biomass accessible to fisheries. Three logistic curves and one additional scenario were used (Figure 3.5). Each logistic curve was defined by the same selectivity value (S), S=1%, for TL=2, and by the trophic level where S is equal to 50%, noted TL_{50} (i.e., "trophic level at first catch", in analogy to the mean length at first capture; Beverton and Holt, 1957).
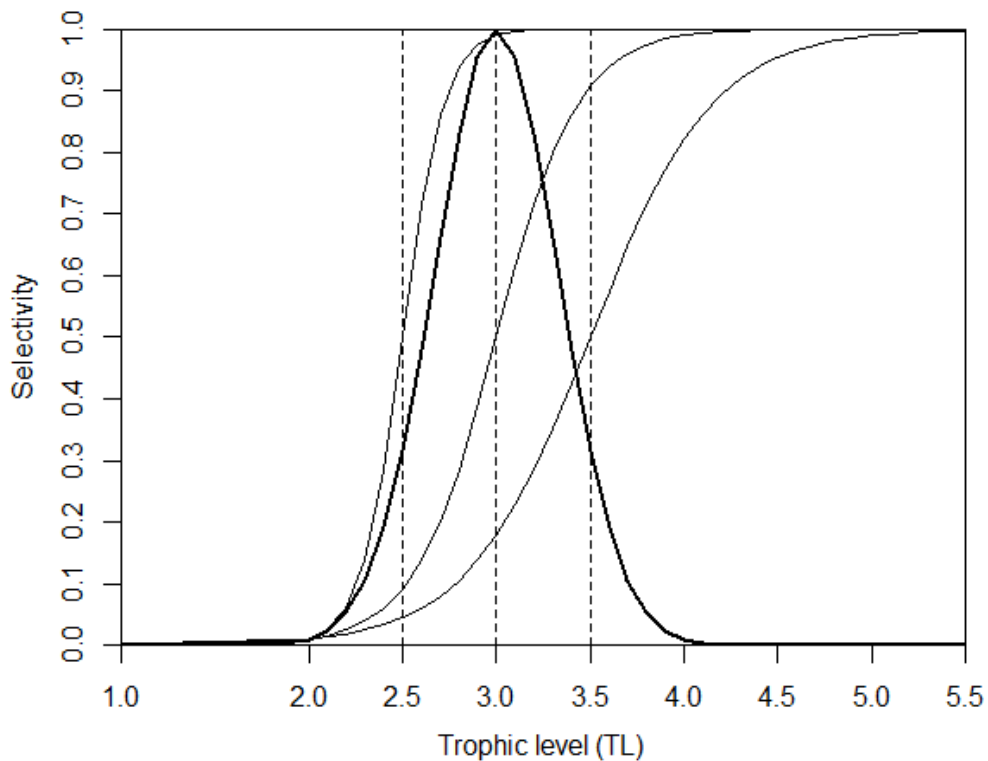
Figure 3.5 Selectivity curves (function of the TL class) used to generate fishing patterns applied to the virtual ecosystem: bold curve corresponds to the scenario centered on TL=3 and dotted lines to the different TL_{50} used to compute the three logistic scenarios.

The reference scenario referred to a medium trophic level at first catch using TL_{50}=3.0; alternative scenarios corresponded to lower (TL_{50}=2.5) or higher (TL_{50}=3.5) values. An additional scenario was also developed with a selectivity curve based on a normal distribution centered on TL=3.0 (S=100%) with S=1% for TL=2 and 4. Such a curve mimics for instance a fishery targeting only small pelagic fishes. All selectivity curves had null values for TL=1. The same fishing mortality F* applied to the accessible biomass was used for all trophic levels. Thus, the fishing mortality applied to the whole biomass ($F = F^* \times S$) followed a logistic curve (or

was centered on TL=3 for the additional scenario). F* varied between 0 (no fishing) and 1 (strong fishing) in simulations, with F*=0.5 being considered as the reference scenario.

For each selectivity curve and analysis (see below), different trophic spectra and indices were computed. Impacts on trophic flows were analyzed using the biomass, production and kinetic trophic spectra. The resistance to fishing was also assessed using indices derived from the biomass and catch trophic spectra. The analysis was separated in three parts (Table 3.1):

- Sensitivity to the foraging arena modifier parameters:

First, the sensitivity of EcoTroph predictions to the two new parameters of the H modifier, ω and G (Eq. (3.19)), was tested. The reference fishing scenario was applied to the virtual ecosystem assuming a null top-down effect (see Table 3.1). Since trophic flows are mainly the consequence of predation, ω was supposed to be low and three values were tested (ω=0, 0.1, 0.2). For G, values ranging between 2 and 40 were applied. The simulated biomass and catch trophic spectra were computed for each combination of parameters, for the unexploited ecosystem, and for the reference fishing scenario without including foraging arena controls.

- Sensitivity to exploitation patterns:

Then, the impact of different theoretical exploitation patterns was investigated along with top-down and foraging arena controls. The four selectivity curves associated with different F* (between 0 and 1) were applied. Five EcoTroph parameterizations were set up: one without top-down and foraging arena controls, two with top-down but no foraging arena controls, two with foraging arena but no top-down controls (see Table 3.1). Different trophic spectra and ratios were computed to assess impacts on the ecosystem trophic flows and resistance: the biomass, production, and kinetic trophic spectra, B/B^0 and $B_{TL \geq 3.3}/B^0_{TL \geq 3.3}$ ratios (ratios of the total biomass and predator biomass, conventionally referring to TLs$\geq$3.3, compared to the unexploited

state), mean trophic levels of the predator and total biomasses, and mean trophic levels of the predator and total catches.

- Sensitivity to TL-dependent effects:

The last step of the virtual ecosystem analysis was to consider trophic level-dependent effects for top-down and foraging arena controls. In fact, top-down controls are not constant across trophic levels. They are mainly due to predators, differ between ecosystems and can lead to trophic cascades (Andersen and Pedersen, 2010; Baum and Worm, 2009; Borer et al., 2005; Casini et al., 2009). These considerations are also valid for foraging arena controls but there is no consistent pattern related to trophic levels. Low G values are usually observed for higher TLs that tend to be more sensitive to fishing, show weaker compensatory response when fished, and forage over wide range habitats (Ahrens et al., 2012; Walters et al., 1997). Four different scenarios were tested for each type of control (Figure 3.6), along with simulation without any control. Cross effects of top-down and foraging arena controls were not analyzed together, but separately following the same design (Table 3.1): no effect, a constant standard effect across trophic levels, a strong effect for low TLs and weak for high TLs, and a strong effect concentrated on TL=3 (Figure 3.6). The different trophic spectra and ratios used to assess impacts on the ecosystem trophic flows and resistance were computed.

Table 3.1 Detailed parameterization of the three different theoretical analyses regarding the fishing scenario (F* and TL$_{50}$), top-down (α) and foraging arena (ω and G) controls used in simulations.

	Fishing scenario		Top-down control	Foraging arena control	
	F*	*TL$_{50}$*	*α*	*ω*	*G*
1. Sensitivity to the foraging arena parameters	0.5	3.0	not included	not included	
			not included	0 0.1 0.2	2 to 40
2. Sensitivity to the exploitation patterns	0 to 1	2.5 3.0 3.5 centered on TL=3	not included	not included	
			0.4 0.8	not included	
			not included	0.1	5 20
3. Sensitivity to TL-dependent effects	0 to 1	3.0	not included	not included	
			0.4 centered on TL=3 exponential decrease step decrease	not included	
			not included	0.1	10 centered on TL=3 exponential increase step increase
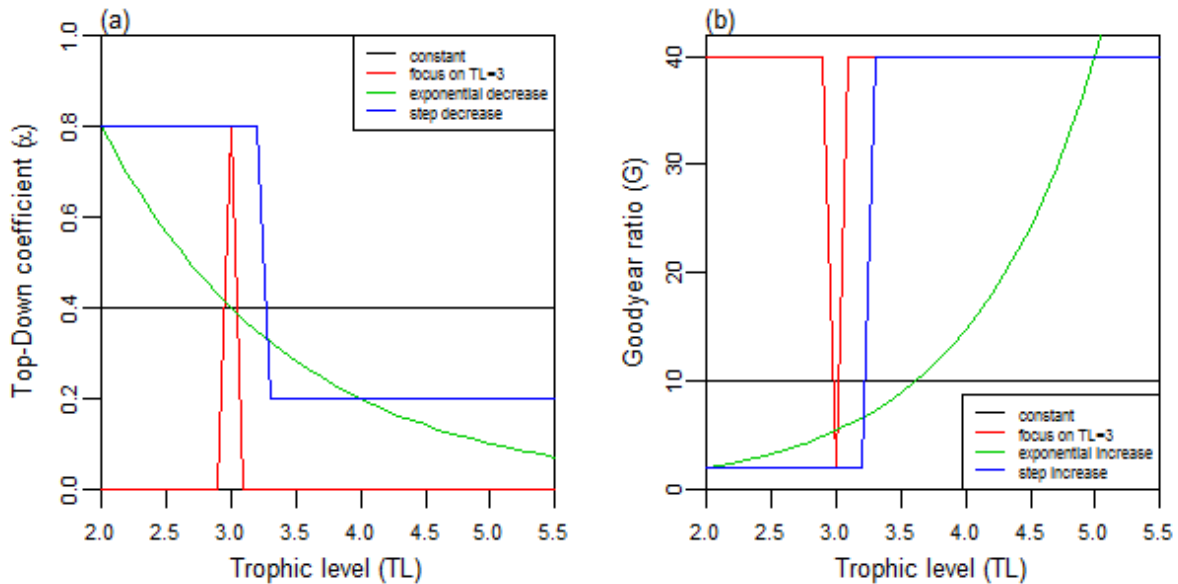
Figure 3.6 Four scenarios developed to test the sensitivity to TL-dependent effects for (a) top-down (on the top-down coefficient α) and (b) foraging arena controls (on the Goodyear compensation ratio G).

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3.4.3 Application to case studies

In a second step, EcoTroph was applied to analyze three real ecosystems which have been previously modeled using EwE. Three models representing different ecosystem types and patterns of fishing changes were selected: one EwE model corresponding to a pelagic environment, the central North Pacific (CN-Pacific; Cox et al., 2002a, 2002b), and two models representing mixed environments, the Gulf of Thailand (Go-Thailand; FAO/FISHCODE, 2001) and the Guinean continental shelf (CS-Guinea; Gascuel et al., 2009a), since patterns associated with foraging arena parameterization were supposed to be different considering differences in predator-prey relations in these ecosystem types. In fact, low G values seem to be more common in pelagic environments where trophic interactions are less limited by spatial/temporal separation in prey and predator species. In contrast, high G values are seen for species that occupy specialized habitats (e.g., reef) and thus have very limited access to prey resources that come into those habitats from larger areas (Ahrens et al., 2012; Walters and Martell, 2004). But these patterns are not always consistent. Furthermore, each EwE model had previously been developed to simulate different historical fishing effort changes (Table 3.2):

- The CN-Pacific EwE model has been developed to assess the trophic impacts of fishing and associated effects on tuna dynamics. The Ecopath model represented the trophic ecosystem during the 1990-1998 period, and has been used to parameterize a dynamic Ecosim model reflecting historical fishing effort changes from 1928 to 1998. This period was separated in two components: the ecosystem model was simulated as unexploited from 1928 to 1952, and then fitted on fishing effort data from 1952 to 1998 (Cox et al., 2002a, 2002b).

- The Go-Thailand EwE model was designed to study bio-economic aspects of the demersal fisheries. The Ecopath model represented the trophic ecosystem in 1973, and the Ecosim model the 1973-1995 period using historical fishing effort changes. During this period, demersal fisheries' effort increased with the development of trawl fisheries that greatly impacted the resources (FAO/FISHCODE, 2001).

- The CS-Guinea EwE model was developed to evaluate fishing impacts on the marine Guinean ecosystem. An Ecopath model was developed to represent the whole ecosystem in 1985 when fishing pressure was relatively low, and an Ecosim model to dynamically reproduce the intensification of fishing effort and related trophic impacts from 1985 to 2004 (Gascuel et al., 2009a). This model was also used to study artisanal and industrial fleets own impacts, but also interactions and trade-offs when managing both fisheries (Gasche and Gascuel, 2013).

These models were selected based on several criteria to ensure homogeneity between Ecosim and EcoTroph procedures. Each Ecosim model was originally parameterized using fishing effort time series and no environmental data as forcing functions, since EcoTroph only accounts for fishing changes. Moreover, no mediation functions were used in Ecosim. Finally, they represented different ecosystem types (see above), and different patterns of fishing changes: simulation of the unexploited state for the CN-Pacific EwE model, strong increase in the fishing effort for the CS-Guinea model, and increase in demersal fisheries effort for the Go-Thailand model.

Table 3.2 Parameters of three EwE models used in this study.

	EwE models		
	Central North Pacific (CN-Pacific)	*Gulf of Thailand (Go-Thailand)*	*Guinean continental shelf (CS-Guinea)*
Reference	(Cox et al., 2002a, 2002b)	(FAO/FISHCODE, 2001)	(Gascuel et al., 2009a)
Source	www.ecopath.org (EcopathMSY database)	www.ecopath.org (EcopathMSY database)	available upon request (didier.gascuel@agrocampus-ouest.fr)
Represented year of the base Ecopath model	1990-1998	1973	1985
Simulated year extracted from Ecosim	1951	1995	2004
Associated changes in Ecosim fleets fishing effort (expressed as effort multipliers) used in EcoTroph simulations	Domestic longline: 0 Domestic purse: 0 Pole and line: 0 Troll: 0 Drift net: 0 Foreign longline: 0 Foreign purse: 0 Other: 0 Turtle egg harvest: 1	Otter board trawl: 2.412 Pair trawl: 1.704 Beam trawl: 0.090 Pushnet: 1.479 Purse seine: 1.916 Other gears: 1.704	Small scale fishery: 8.967 Industrial fishery: 5.151

Since the three EwE models were all available with vulnerabilities by default set to 2, the Ecosim models were adjusted following a standard methodology (V. Christensen, UBC Fisheries Centre, pers. comm.). Each model was fitted to time series using a routine that search groups' vulnerabilities (see Section 3.4.1) to reduce the sum of squared residuals compared to the supplied time series of biomass, catches or mortality. More precisely, only the groups with time series were searched, since this method seemed more precautious and avoided searching groups with no information (i.e., no time series) that can lead to unrealistic predictions (Christensen et al., submitted). Then, the annual biomasses, trophic levels and mortalities (Z) were extracted from the best fitted Ecosim simulation (coming from the three EwE models), and associated trophic spectra were computed. In parallel, an EcoTroph model of the base Ecopath model was

computed for each EwE model, and used to run simulations considering the same changes in fleets fishing effort for a specific year as in Ecosim (Table 3.2). These simulations were done using different values of α, ω, and G. All combinations of α ranging between 0 and 1 (step of 0.1; a null value corresponds to simulations without top-down controls), ω between 0 and 0.3 (step of 0.1), and G between 2 and 40 (step of 1) were tested, along with the simulations without foraging arena controls. For each simulation, the sum of squared residuals (SSR; Eq. (3.20)) by trophic class of the simulated biomass trophic spectra compared to the Ecosim prediction was calculated:

$$SSR = \sum_{\tau=2}^{\tau=5.5} (log(B_\tau^{ET}) - log(B_\tau^{EwE}))^2 \qquad (3.20)$$

where $B_\tau^{ET}, B_\tau^{EwE}$ corresponded respectively to the biomass of the trophic class $[\tau, \tau+\Delta\tau[$ in the EcoTroph and Ecosim simulations. This enabled to compare EcoTroph and Ecosim predictions for the three EwE models, and to analyze impacts of ET parameterization.

3.5   Results

3.5.1   Virtual ecosystem analyses

Analysis of the sensitivity to the two new parameters of the H modifier, ω and G (Eq. (3.19)), showed that simulations were highly sensitive to G (Figure 3.7). Fishing impacts simulated using the reference scenario differed between tested G values, with a greater impact for low G and ω values. The most impacted biomass trophic spectra compared to the unexploited state was observed for ω=0 and G=2, with a biomass almost null for TLs≥3. This scenario appeared unreasonable; on the other hand, a G value of 40 caused the model to predict similar

impacts as the EcoTroph formulation without foraging arena trophic controls. Differences in fishing impact concentrated on high trophic levels (TLs≥3.5), since TLs between 2 and 3.5 were impacted for the lowest G values only. Simulated catches remained close except for G values of 2 and 5 that exhibited lower catches due to the high biomass decrease for intermediate and high TLs.
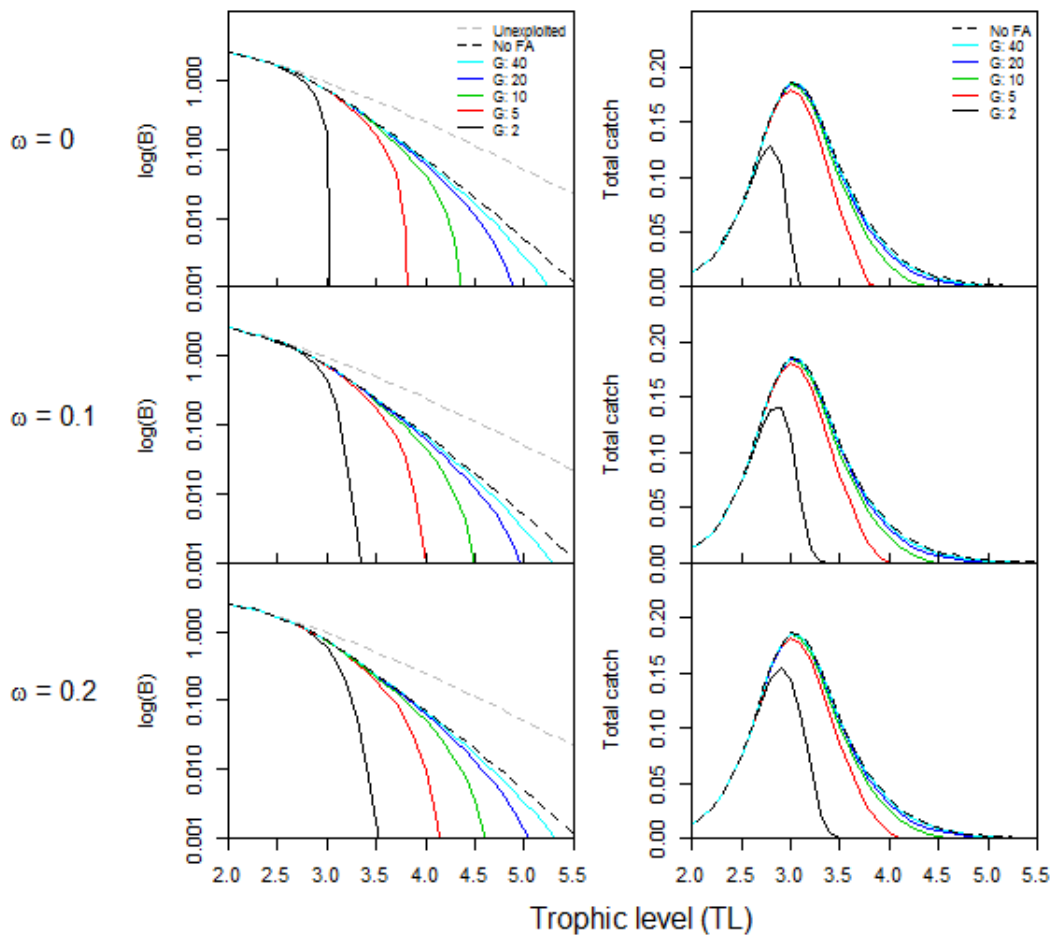
Figure 3.7 Biomass trophic spectra (log scale) simulated using the reference fishing scenario. Solid lines refer to the different simulations including foraging arena controls; black dashed line refers to the simulation without foraging arena (FA) control; and grey dashed line to the unexploited ecosystem.

Then, effects of trophic controls aside, the various exploitation patterns impacted differently the unexploited ecosystem (Figure 3.8 and Figure 3.9, left column). A fishery scenario targeting a broader part of the ecosystem (TL_{50}=2.5) had greater impact on the relative predator and total biomass (respectively 80% and 30% decreases compared to the unexploited state for F*=1) than a fishery scenario targeting only predators (TL_{50}=3.5; respectively 60% and 10% decreases). The mean TL of the biomass was also more impacted when the trophic level at first catch was low (Figure 3.8). Logically, the additional fishing scenario centered on TL=3 showed a greater impact on biomass for TLs around 3 but lower impacts for high TLs (Figure 3.9, top plots). In fact, the relative predator biomass was slightly impacted, and the mean TL of predator biomass increased due to a greater biomass decrease for TLs around 3 (predator biomass starts conventionally at TL=3.3) compared to higher TLs (Figure 3.8). These results showed that the simulated unexploited ecosystem resisted a fishing scenario targeting only predatory fishes or a specific TL range (additional fishing scenario) better when top-down or foraging arena controls were not taken into account.

Inclusion of foraging arena controls (Figure 3.8 and Figure 3.9, second and third columns) caused the model to predict greater impacts for all the different exploitation patterns. These impacts concentrated on high TLs, and were more important considering a strong effect of foraging arena controls (low G value; G=5). Overall, foraging arena controls resulted in less resistant ecosystems. The fishery scenario targeting a broader part of the ecosystem (TL_{50}=2.5) still had greater impact compared to the two others scenarios. Lower predator catches (reaching plateaus for lower F*) and lower total catches were observed in all cases, due to lower relative predator biomasses (compared to the left column, Figure 3.8). The additional fishing scenario biomass trophic spectra showed a strong biomass decrease for high TLs following the fishing

impact on TLs around 3.0. This was different from the previous simulation not accounting for foraging arena controls (Figure 3.9).

On the other hand, inclusion of top-down controls (Figure 3.8 and Figure 3.9, fourth and fifth columns) caused the model to predict relative similar impacts for high TLs compared to the EcoTroph formulation without foraging arena and top-down trophic controls. The relative predator biomass and mean TL remained close, whereas relative biomass increased for high F^* (Figure 3.8). These differences showed a greater resistance to fishing impact in term of total biomass. They were explained by a higher biomass for lower and intermediate TLs due to top-down controls, i.e., the release in predation caused by the fishing induced decrease in predator biomass (see biomass trophic spectra, top plots, Figure 3.9). The range of the biomass increase differed between the different fishing scenarios, appearing for low TLs with $TL_{50}=2.5$ and a fishing scenario centered on TL=3, around TL=2.5 for $TL_{50}=3.0$, and around TL=3 for $TL_{50}=3.5$. This was explained by the fact that top-down controls are function of the predator biomass, and that fishing scenarios impacted different TL ranges depending on TL_{50}.
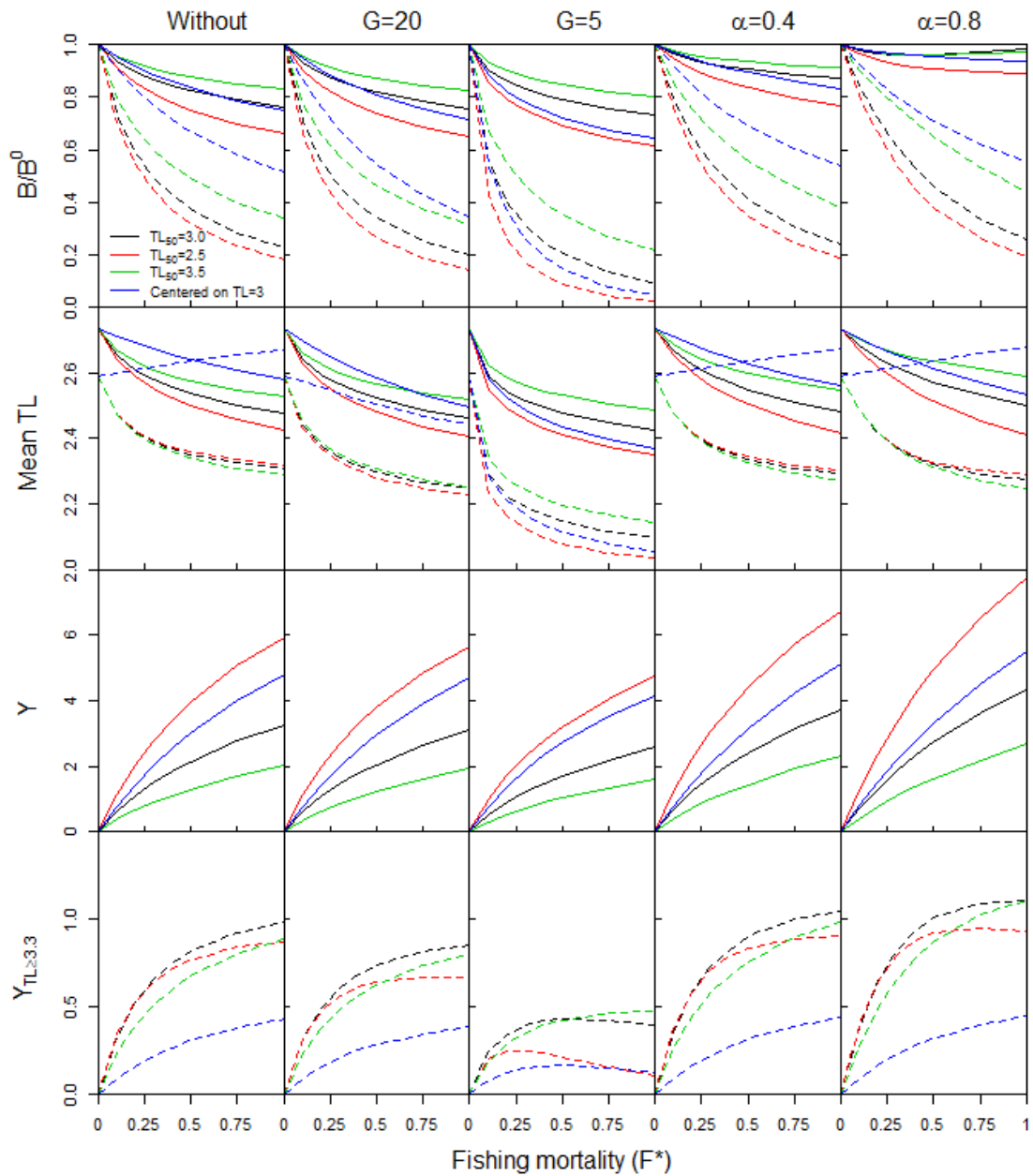
Figure 3.8 Value of EcoTroph outputs function of the fishing mortality (F*) used in simulation: the relative biomass and predator biomass ratios (B/B^0 and $B_{TL\geq3.3}/B^0_{TL\geq3.3}$, dashed lines for predator variables), the mean trophic level of the biomass and predator biomass, the total catch (Y), and the predator catch ($Y_{TL\geq3.3}$). The left column refers to ET simulations without top-down and foraging arena controls, the subsequent two refer to ET simulations including only foraging arena controls ($\omega=0.1$ and G=20 and 5), and the two right columns to ET simulations including only top-down controls ($\alpha=0.4$ and 0.8).

EcoTroph simulations showed the impact of top-down and foraging arena controls on the flow kinetic K, and the biomass flow (using the production P) (Figure 3.9). The H modifier function of TL followed sigmoid curve, and showed greater impacts for higher TLs. The inflexion point and the steepness of the curve were determined by the fishing scenario and mortality used in the analysis, the H modifier tending to ω for the highest TLs (see Eq. (3.19)). As a result, foraging arena controls few impacted the flow kinetic but rather the biomass flow with important losses of production. On the other hand, top-down controls impacted directly the flow kinetic, but not the biomass flow. It introduced a compensatory mechanism for low TLs, exploitation being at least partially compensated by a release in predation. In parallel, predators benefited from this increase in prey abundance as a feedback effect.
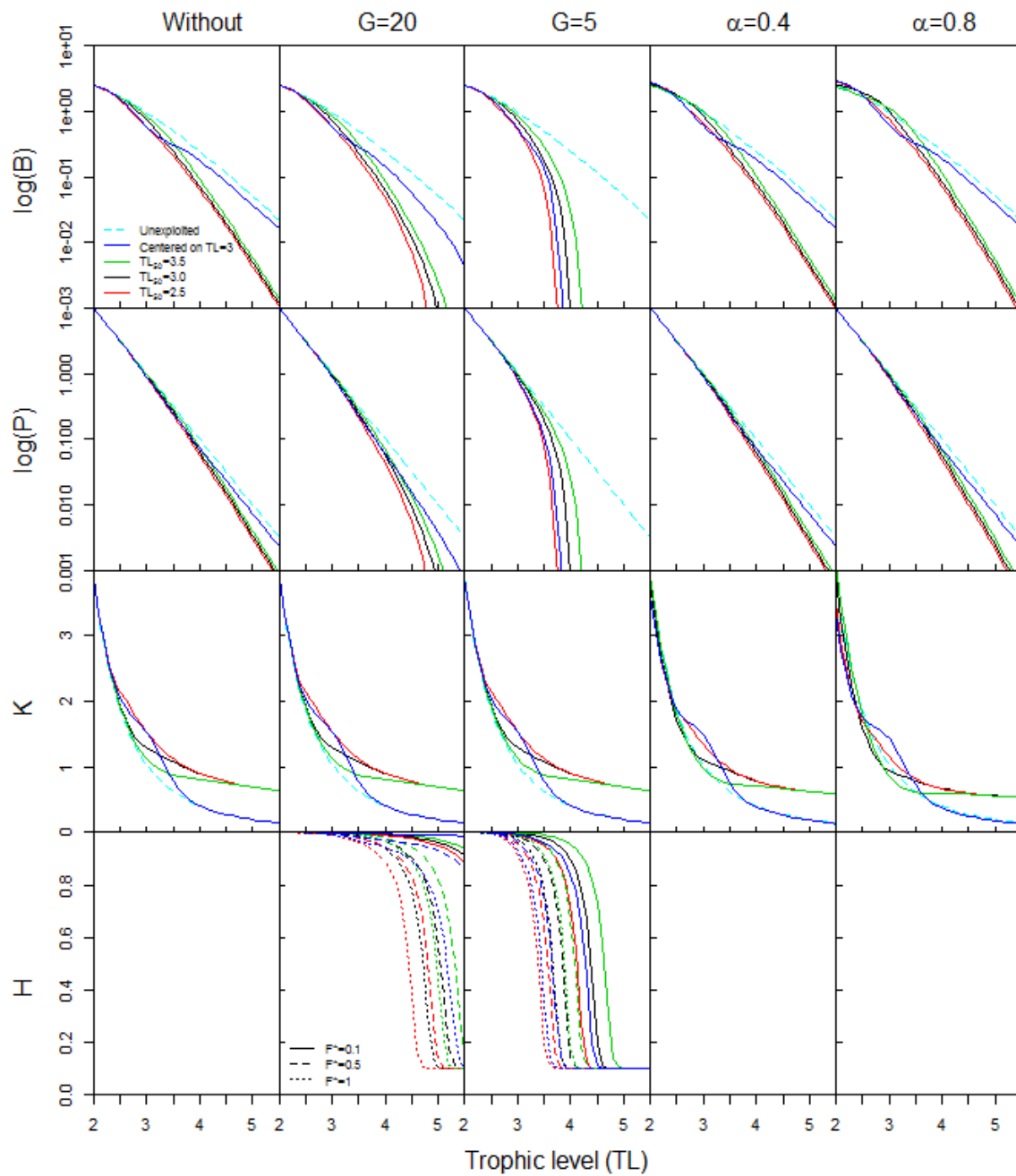
Figure 3.9 Trophic spectra of the biomass, the production, the kinetic (for F*=0.5), and the H modifier (for F*=0.1, 0.5 and 1) considering different exploitation patterns and EcoTroph simulations. The left column refers to ET simulations without top-down and foraging arena controls, the subsequent two refer to ET simulations including only foraging arena controls (ω=0.1 and G=20 and 5), and the two right columns to ET simulations including only top-down controls (α=0.4 and 0.8).

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Finally, trophic level-dependent effects for the top-down and foraging arena controls were considered. The effect of a TL-dependent top-down control (Figure 3.6a) appeared weak for high trophic levels since biomass trophic spectra were similar for these TL classes (Figure 3.10, top plots). On the contrary, increases in biomass for low and intermediate TLs (2.3≤TL≤3.5) were observed, with even greater values compared to the unexploited state. The amplitude of such increases was determined by the strength and the range of the top-down controls: the biomass increase was limited to TL=3 for a top-down effect focusing on that specific TL class, whereas it covered a broader TL range (2.3≤TL≤3.3) using a step increase in α values. Exponential increase and constant scenarios for α values were slightly different, they crossed at TL=3 following both α patterns (see Figure 3.6a). More precisely, impacts concentrated on the K values (flow kinetic) rather than production values (biomass flow) that changed little in the different simulations (Figure 3.10). Strong top-down controls for low and intermediate TLs decreased K values compared to the unexploited state. Overall, this resulted in similar indices regarding predators' resistance, but strong top-down controls determined more resistant ecosystems in terms of total biomass and associated catches (see Appendix D).

In contrast, the effect of a TL-dependent foraging arena control (Figure 3.6b) concentrated on intermediate and high trophic levels with important biomass decreases. Biomass trophic spectra (Figure 3.10) were similar for low TLs (2≤TL≤2.5) but patterns differed for higher TLs. The different G scenarios determined the amplitude and range of observed biomass decreases. Considering a strong foraging arena control on TL=3 resulted in lower biomasses for TLs≥3. A huge decrease in biomass was observed with a step increase in G_τ. Exponential decrease and constant scenarios for G values were slightly different, they crossed at TL=4.2 following both G patterns with a TL-shift due to the propagating effect of foraging arena

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controls. More precisely, foraging arena controls concentrated on the biomass flow (production) with changes determining biomass trends (Figure 3.10). As a consequence, different EcoTroph indices were observed showing that strong foraging arena controls determined less resistant ecosystems in terms of total biomass, catches and predator ratios (see Appendix D).
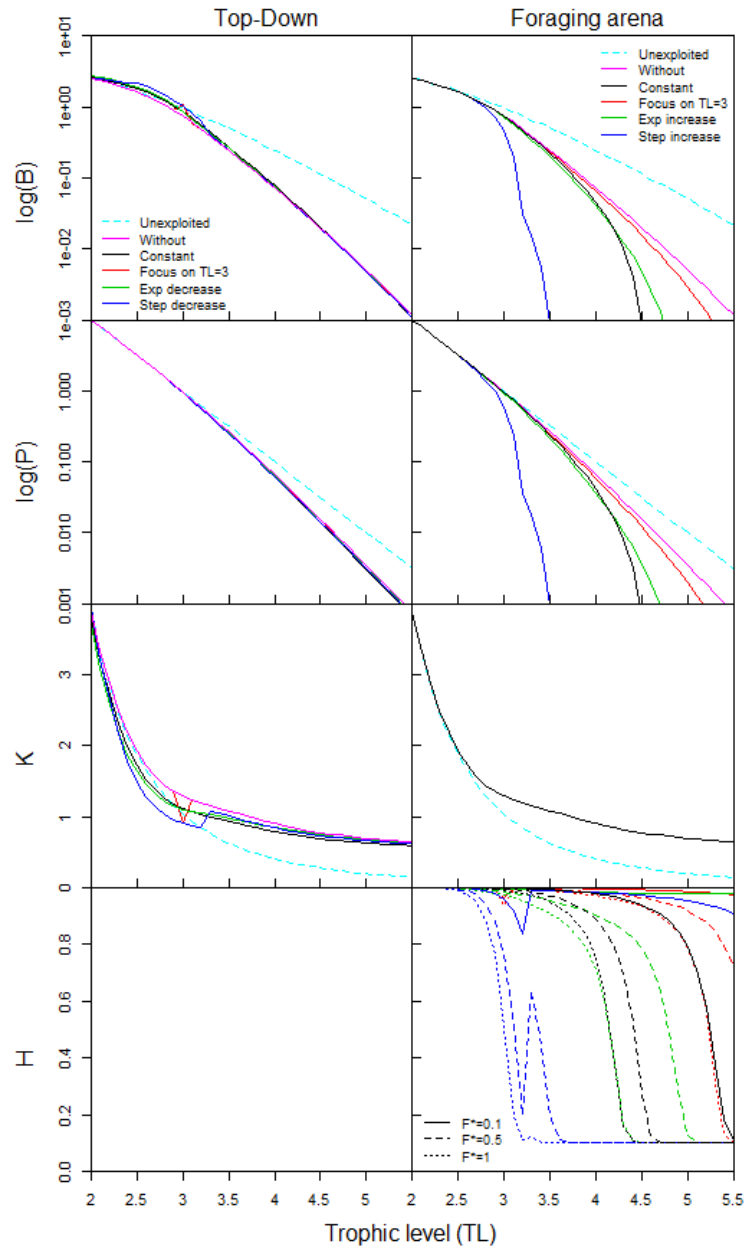
Figure 3.10 Trophic spectra of the biomass, the production, the kinetic (for F*=0.5), and the H modifier (for F*=0.1, 0.5 and 1) considering different TL-dependent effects. The left and right columns refer respectively to the different EcoTroph simulations with varying top-down and foraging arena control scenarios. The different TL-dependent effects are represented using black for scenarios where controls are constant over TLs, red where controls focus on TL=3, green where controls exponentially increase over TLs, and blue where controls step increase with strong controls for high TLs only. The simulated unexploited ecosystem (dashed light blue line), and the simulated exploited ecosystem without foraging arena and top-down controls (purple line) are also represented.

3.5.2 Application to case studies

The virtual ecosystem analysis raised the questions of ET application to real case studies, and the best parameterization to simulate realistic fishing impacts. Figure 3.11 showed that patterns differed between the three real ecosystems. The best fit when simulating the CN-Pacific at an unexploited state (as the year 1951 in the Ecosim dynamic model) were obtained for low G values and no top-down controls (α=0). The lowest SSR values were highly localized, and the best adjustment was obtained for ω=0, G=7 and α=0. Looking at the ten best adjustments parameterization (over 1727 tested combinations, Table 3.3), it appeared that the fitting procedure was few sensitive to ω values but mostly to G and α values ($5 \leq G \leq 8$, α=0 in all cases). In fact, the Ecosim model predicted an important biomass increase for TLs$\geq$3.5 compared to the Ecopath model of the recent period (Figure 3.12). The inclusion of foraging arena controls enabled EcoTroph to better reflect this increase in biomass at the unexploited state. However, EcoTroph tested parameterizations were unable to model such an increase as observed in Ecosim for TLs lower than 5. More precisely, ET was able to better simulate the increase in production at the unexploited state, but unable to simulate a sufficient decrease in kinetic as observed in Ecosim (Figure 3.12).Thus, strong foraging arena controls (low G values) enabled to better model and understand the increase in production for the high TLs.
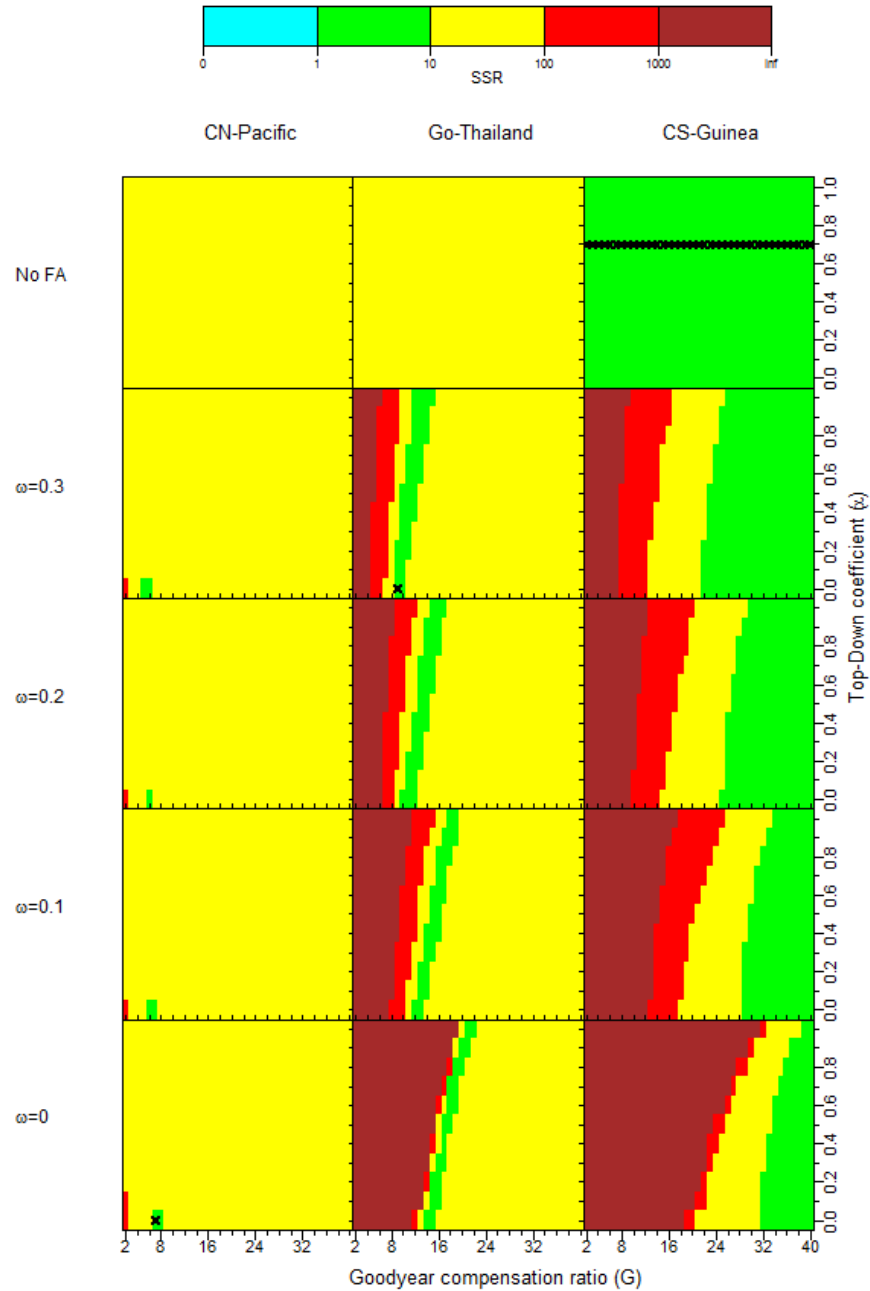
Figure 3.11 Plots of the sum of squared residuals (SSR) between Ecosim and EcoTroph predictions for the central North Pacific (CN-Pacific; Cox et al., 2002a, 2002b), Gulf of Thailand (Go-Thailand; FAO/FISHCODE, 2001) and Guinean continental shelf (CS-Guinea; Gascuel et al., 2009a) EwE models. SSR is function of the top-down coefficient (α) and the Goodyear compensation ratio (G) for the different tested ω values. The best adjustment is represented with a black cross. For the simulations done without foraging arena controls, a solid line (covering all tested G values) corresponds to one simulation.

Table 3.3 EcoTroph parameters (i.e., ω and G parameters for foraging arena controls, and α for top-down controls) giving the ten best fits (lower sum of squared residuals SSR) compared to Ecosim predictions.

	CN-Pacific				Go-Thailand				CS-Guinea			
	ω	*G*	*α*	*SSR*	*ω*	*G*	*α*	*SSR*	*ω*	*G*	*α*	*SSR*
1	0	7	0	9.786	0.3	9	0	3.412	not included		0.7	1.446
2	0.2	6	0	9.817	0.3	10	0.3	4.196	not included		0.8	1.454
3	0.3	5	0	9.820	0.3	10	0.2	4.291	not included		0.6	1.460
4	0.1	6	0	9.833	0.3	11	0.5	4.404	not included		0.9	1.484
5	0.1	7	0	9.844	0.1	12	0	4.510	not included		0.5	1.496
6	0	8	0	9.878	0.3	11	0.6	4.656	not included		1	1.535
7	0.3	6	0	9.972	0.3	12	0.8	4.706	not included		0.4	1.552
8	0.2	7	0	10.011	0.2	12	0.3	4.895	not included		0.3	1.629
9	0.2	5	0	10.014	0.2	11	0	4.904	not included		0.2	1.727
10	0.1	8	0	10.044	0.3	12	0.7	4.945	not included		0.1	1.847
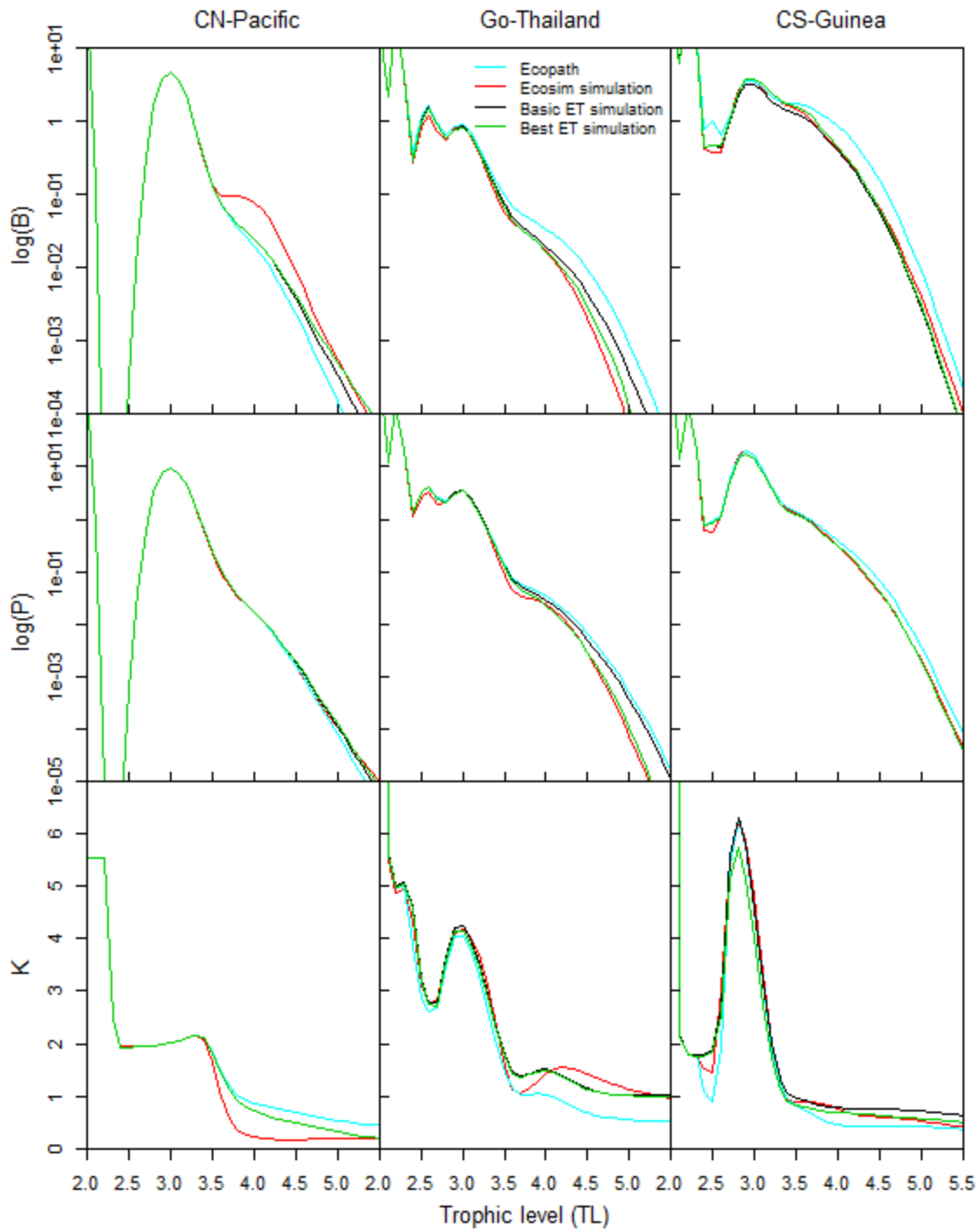
Figure 3.12 Trophic spectra of the biomass, the production, and the kinetic of the base Ecopath model, the Ecosim prediction, the ET prediction without top-down and foraging arena controls, and the best ET prediction (corresponding to the minimum SSR parameterization) for the three case studies.

The Go-Thailand case study exhibited a different behavior. In fact, SSR values appeared very sensitive to G values, but much less to α and ω values (Figure 3.11). The best fit was obtained for ω=0.3, G=9 and α=0. Looking at the ten best fits (Table 3.3), ω values were comprised between 0 and 0.3, α between 0 and 0.8, and G between 9 and 12. Low G values, as observed for the CN-Pacific model, caused the model to greatly diverge from the Ecosim prediction. Accounting for foraging arena controls enabled EcoTroph to better predict the decrease in biomass as observed for intermediate and high TLs in Ecosim (Figure 3.12). EcoTroph was less sensitive to the different α values since they determined a better fit over different TL classes. Inclusion of the H modifier enabled to better fit the loss of production due to the increase in fishing effort, as observed in Ecosim (Figure 3.12). However, EcoTroph and Ecosim simulated kinetics were different. The inclusion of constant top-down controls was not sufficient to explain the similar kinetic of Ecosim and Ecopath models observed around TL=3.6. On the contrary, the increase in kinetic for high TLs (due to the increase in fishing effort) was consistent with EcoTroph predictions.

Finally, the CS-Guinea model showed a relative common pattern with the Go-Thailand model: SSR values appeared highly sensitive to the G values (and more precisely, inclusion/exclusion of foraging arena controls), but less sensitive to α and ω values (Figure 3.11). In fact, the best adjustment was obtained assuming no foraging arena and strong top-down controls (α=0.7). The ten best adjustments all corresponded to an EcoTroph parameterization not accounting for foraging arena controls, and covered all positive α values (0.1≤α≤1). EcoTroph enabled to model the decrease in predator biomass, and the inclusion of top-down controls enabled to understand the relative similar biomass for intermediate TLs compared to the Ecopath biomass trophic spectra (Figure 3.12). This was due to the fact that the EcoTroph production

equation without foraging arena controls was sufficient to explain the loss in production for high TLs (but not for TL=2.5, see Figure 3.12). Constant top-down controls enabled to better model the kinetic for high TLs. This was not the case for the intermediate TLs since EcoTroph kinetic equation predicted a decrease that was not observed in Ecosim or the EcoTroph parameterization without trophic controls. Thus, accounting for top-down controls enabled to better fit kinetic changes caused by the increase in fishing effort, as observed in the CS-Guinea EwE ecosystem model.

In conclusion, results showed that inclusion of top-down and foraging arena controls enabled a better simulation of fishing impacts on ecosystems (increase or decrease in fishing effort). Constant trophic controls (over the different TL classes) were tested, and showed that the inclusion of foraging arena controls enabled to better fit changes in production due to direct and indirect fishing impacts, as modeled in Ecosim. It caused the ET model to predict more important losses or gains in production with respectively an increasing or decreasing fishing effort. On the other hand, inclusion of top-down controls seemed to enable a better representation of fishing induced changes (direct and indirect) in kinetic. However, precise changes as modeled in Ecosim were not well matched using tested parameterizations. The CN-Pacific pelagic ecosystem model exhibited strong foraging arena controls (low G values) but no top-down controls in order to fit the Ecosim model. On the contrary, mixed ecosystems as the Go-Thailand and CS-Guinea tended to have higher G values (even no foraging arena control for the CS-Guinea ET model), and exhibited top-down controls.

3.6   Discussion

3.6.1   Foraging arena and top-down controls

Ecosystem modeling constitutes an important research area that is still being improved by the inclusion of complex processes and simulation procedures to evaluate fishing impacts. In the present chapter, results showed that accounting for two important trophic mechanisms, top-down and foraging arena controls, can have important consequences on ecosystem models and associated predictions. In fact, inclusion of top-down and foraging arena controls in the EcoTroph ecosystem model impacted the trophic flows and the resistance of a virtual ecosystem exposed to different fishing scenarios. This impact differed between the different fishing scenarios: the stronger and broader the fishing pressure was, the more important effects were on biomass and production, and the resulting impacts of top-down and foraging arena controls. Results emphasized the greater loss of production and resistance when accounting for foraging arena controls. On the other hand, top-down controls affected the kinetic of biomass flows, and increased the resistance to fishing impacts. These changes in production and kinetic were also TL-dependent since different scenarios of trophic control affected differently the TL classes.

EcoTroph simulations accounted for the impacts of top-down controls (Eq. (3.11)) on ecosystem trophic flows; the extent to which top-down control occurs is an important element of ecosystem functioning. It may not replace bottom-up control, but occurs simultaneously in real ecosystems (Borer et al., 2005; Cury et al., 2000; Hunter and Price, 1992). Since all animals need to eat prey, bottom-up relationships always intervene and were always considered in the model (Gascuel and Pauly, 2009). Conversely, preys are impacted by predator abundance, but this reciprocal relationship may not always apply since prey may experience little predation,

depending on their behavior (Walters et al., 1997). When top-down control was considered in EcoTroph simulations, fishing at a given TL impacted all other TLs by notably inducing a biomass increase at lower TLs. As fishing reduced the biomass of predators responsible for top-down controls, it slowed down prey flows, increasing their life expectancy. Such a pattern has been observed frequently in real ecosystems, and is often considered as a major indirect effect of fishing (Baum and Worm, 2009; Goñi, 1998; Jennings and Kaiser, 1998). Results showed that top-down controls could lead to limited fishing impacts on the total biomass, even for the heaviest rates of exploitation, as a result of the increase in prey abundance. In other words, top-down controls could be considered as a compensation mechanism, increasing the overall resistance of ecosystems to fishing. Nevertheless, as fishing pressure increased, the simulated ecosystems changed. Top predators were the most impacted, and the mean TL of the remaining biomass decreased. Such a change constitutes a loss of functional biodiversity (Pauly and Watson, 2005). As a consequence, resistance induced by top-down control could be limited since it vanished when exploitation rates were too high. In that case, predators disappeared and bottom-up controls became dominant. Therefore, the fishery-induced loss of top predators may change ecosystem trophic controls, the ecosystem becoming more unstable and more dependent on environmental conditions (Baum and Worm, 2009; Jackson et al., 2001). Such changes have been observed both in theoretical simulations based on a dynamic version of EcoTroph (Gascuel and Pauly, 2009), and in specific ecosystems (e.g., Gascuel et al., 2007). Ecosystem models constitute a useful tool to study these aspects. This analysis showed that they have the capability to mimic and explain observed changes, as modeled in EcoTroph through the integration of the α parameter. The effect of top-down controls on the trophic class $[\tau+\Delta\tau[$ was determined by α_τ values and changes in biomass due to fishing at TL $\tau+1$. Different values and shape for this

parameter were tested and showed sensitivity regarding fishing impacts and ecosystem indices. It is therefore recommended to conduct sensitivity analyses when applying EcoTroph to real ecosystems, in order to understand possible impacts of strong/weak top-down controls on ecosystem functioning.

The analysis also accounted for the impacts of foraging arena controls (Eq. (3.18)) on ecosystem trophic flows in conjunction with fishing impacts. Foraging arenas appear common in aquatic ecosystems and cover a wide variety of mechanisms (see review in Ahrens et al., 2012). Results showed that including such a trophic control increased predicted impacts of fishing, and resulted in a less resistant ecosystem. In fact, it limited the biomass flow at each TL class compared to the ET formulation without foraging arena controls, where the biomass flow Φ_τ was independent of any reduction effect that fishing may have on that TL class. Furthermore, the inclusion of foraging arena control indicated that exploitation of low TLs could impact importantly high TLs production and biomass, since such control increased the interactions between trophic levels. This was dependent on the G value, a lower value resulting in stronger foraging arena controls. This showed that the effect of foraging arena controls propagated through TL classes, i.e., the loss of biomass flow in one TL class affected higher TL classes. This was also consistent with other studies showing that fishing low trophic level species can have large impacts on other parts of the ecosystem, especially on predators (Smith et al., 2011). It has also been shown that prey numbers decline causes the abundances of marine predators to become more variable (Plagányi et al., 2014). As for the top-down control, an important question was the parameterization of this trophic control. Two new parameters, ω and G, having different characteristics were included. ω was typically assumed to be low since the majority of biomass does not move to higher TLs simply by organisms changing their diet as they grow. ω values

ranging between 0 and 0.3 were tested, and demonstrated little sensitivity to this parameter. On the contrary, impacts on the biomass flow and related fishing effects were very sensitive to the Goodyear compensation ratio (see Appendix C for details on this parameter). Simulations suggested that G should be greater than (or equal to) 5 to simulate reasonable fishing impacts. Values for this parameter depend on species' behaviors, and Ecosim fitting exercises tend to result in lower G values for high TLs, i.e. stronger controls. In fact, high TLs tend to be more sensitive to fishing, show weaker compensatory response when fished, and involve higher vulnerability exchange rate for their prey since they forage over wide range habitats (Ahrens et al., 2012; Walters et al., 1997). Low G values are also more common in pelagic ecosystems, while high G values are usually observed for species occupying specialized habitats (e.g., reef). When integrated at the ecosystem level, no studies have yet assessed G values over trophic level classes for different ecosystem types. In this chapter, different hypothetical values and shapes were tested to first understand impacts of foraging arena control on modeling ecosystem trophic flows and fishing effects. Furthermore, EcoTroph formulation without foraging arena controls assumed the natural losses to be independent of the ecosystem state (i.e., constant μ, see Eq. (3.7)). This is a strong hypothesis since it has been shown that natural losses can vary over time with changes in environment and fishing effort (e.g., Coll et al., 2009). Inclusion of foraging arena control introduces change in natural losses through the H modifier (Eq. (3.19)), and enables the impacts of fishing on μ to be studied.

3.6.2   Use of EcoTroph to analyze ecosystems

Integrating top-down and foraging arena controls enabled a better prediction of fishing impacts on the three real case studies, in relation to Ecosim historical predictions. It was hard to

extract general conclusions considering the restricted number of the case studies. However, results were consistent with the basic predictions on G values (see above). Low G values and no top-down controls were observed for the pelagic CN-Pacific model, whereas the two mixed ecosystems (Go-Thailand and CS-Guinea) showed higher G values and effective top-down controls. More precisely, the Gulf of Thailand adjustment gave G values between 9 and 12, whereas the Guinean case study exhibited a potential low effect of foraging arena control (high G or no foraging arena control included at all). This was maybe due to the fact that the Gulf of Thailand is a shallow ecosystem (maximum depth is around 80m) occupied mostly by demersal species (FAO/FISHCODE, 2001), and thus potentially less limited predator-prey interactions compared to the Guinean continental shelf (maximum depth around 200m) that has important demersal and pelagic biomasses occupying specific ecosystem parts (Gascuel et al., 2009a).

A comparison of biomass trophic spectra indicated that EcoTroph simulation without top-down and foraging arena controls corresponded to the trends observed in Ecosim predictions, but with different amplitudes. Inclusion of trophic controls resulted in a better fit to Ecosim predictions. This improvement was not sufficient to explain changes observed in the CN-Pacific EwE model, since the return of the biomass to an unexploited state was too strong (for predators) to be simulated by EcoTroph using tested parameters. Looking at the production and kinetic trophic spectra, it appeared that the main differences between the best ET adjustment and the Ecosim simulation were explained by differences in the flow kinetic. A possible explanation for such differences is the fact that only constant α_τ values applied to the different TL classes were tested. The use of different top-down control values for the different TL classes (varying α_τ values) could enable a better adjustment, and is logical considering the different trophic properties between TL classes. This could also be implemented for the foraging arena control to

better understand how this control varies between TL classes. Another possible factor is the fact that EcoTroph results referred to steady-state conditions (ET-Diagnosis routine), whereas Ecosim is dynamically fitted on historical time series. A dynamic version of EcoTroph has also been developed (ET-Dynamic; Gascuel et al., 2009b; Gascuel and Pauly, 2009), but it is currently being revised and tested on different case studies. It would be interesting to extend this framework on numerous case studies, with a comparison between Ecosim and ET-Dynamic predictions considering TL-dependent trophic controls. It could enable a better assessment of the shapes and values of α_τ and G_τ, but also dynamically assess their impacts on ecosystem trophic flows and fishing effects. Furthermore, using EcoTroph in order to analyze ecosystem functioning and fishing impacts on applied case studies does not present any particular conceptual difficulties. This is especially the case when EcoTroph is applied in conjunction with an EwE model.

Finally, trophodynamic models as EcoTroph and EwE appear to be useful tools to understand and predict changes at the ecosystem scale associated with different fishing scenarios. Environmental impacts can also be accounted for in Ecopath with Ecosim (also in ET-Dynamic through primary production changes). These models allow for a better understanding of ecosystem properties and trophic functioning. In the present chapter, results have shown that top-down and foraging arena controls increased interactions between trophic levels, and consequently the extent of fishing impacts. This result emphasizes the need for an ecosystem approach to fisheries (Garcia et al., 2003) in order to better assess and predict fishing impacts at the ecosystem scale.

Chapter 4: Fishing inside or outside? A case studies analysis of potential spillover effect from marine protected areas, using food web models

4.1 Summary

Marine protected areas (MPAs) are implemented worldwide as an efficient tool to preserve biodiversity and protect ecosystems. Food web models (Ecopath and EcoTroph) were used to assess the ability of MPAs to reduce fishing impacts on targeted resources and to provide biomass exports for adjacent fisheries. Three coastal MPAs: Bonifacio and Port-Cros (Mediterranean Sea), and Bamboung (Senegalese coast), were used as case studies. Pre-existing related Ecopath models were homogenized and ecosystem characteristics were compared based on network indices and trophic spectra analyses. Using the EcoTroph model, different fishing mortality scenarios were simulated, which enabled to assess fishing impacts on the three ecosystems. Lastly, the potential biomass that could be exported from each MPA was estimated. Despite structural and functional trophic differences, the three MPAs showed similar patterns of resistance to simulated fishing mortalities, with the Bonifacio case study exhibiting the highest potential catches and a slightly inferior resistance to fishing. Results also showed that the potential exports from small size MPAs are limited and thus may only benefit local fishing activities. Based on simulations, their potential exports were estimated to be at the same order of magnitude as the amount of catch that could have been obtained inside the reserve. In Port-Cros, the ban of fishing inside MPA could actually allow for improved catch yields outside the MPA due to biomass exports. This was not the case for the Bonifacio site, as its potential exports were too low to offset catch losses. This insight suggests the need for MPA networks and/or

sufficiently large MPAs to effectively protect juveniles and adults and provide important exports. Finally, the effects of MPAs on fisheries that were not considered in food web models were discussed, as well as possible improvements in the analysis of MPA efficiency.

4.2   Introduction

Human activities are causing unprecedented changes to marine ecosystems, partly through both direct and indirect fishing effects (Halpern et al., 2008; Jackson et al., 2001). The increase in demand for seafood has led to a substantial expansion of fisheries through all the oceans and marine habitats (Pauly et al., 2002; Swartz et al., 2010), at all depths (Morato et al., 2006; Pauly et al., 2003), and toward lower trophic levels (Essington et al., 2006; Pauly et al., 1998). These changes in exploitation cause major changes in biological assemblages and, ultimately, lead to biodiversity losses that may disrupt ecosystem functioning and alter the sustainability of the goods and services provided by the many marine environments that currently support human welfare (Lotze et al., 2006; Pauly and Watson, 2005; Worm et al., 2006).

To protect marine biodiversity and counteract human impacts on marine ecosystems, one intuitive management strategy is to close certain parts of the ocean to fishing. This solution has been employed since the Middle Ages where European kings controlled and closed access to certain streams (Hoffmann, 1996), and was advised as a management tool for fisheries by Hérubel (1912) over a century ago. Nowadays, marine protected areas are implemented worldwide as a tool for an ecosystem approach to fisheries (Garcia et al., 2003), and to meet the objectives defined by the Convention on Biological Diversity (CBD). In 2004, the CBD reached a consensus among partners such that 10% of each ecoregion would be protected before 2010,

the final objective being the creation of a network of protected areas covering the major part of biodiversity by 2012 (CBD, 2004). The 2010 deadline has been extended to 2020 because the target was not met in time. In fact, MPA implementations develop slowly, covering a still limited but larger part of the ocean: 1.6% in 2012 (Dulvy, 2013), and 2.1% in 2014 (http://www.mpatlas.org/).

MPAs are viewed as an effective tool benefiting habitats and fish populations. Not only can they drive increases in the mean size, density, abundance, and species diversity of the various fish populations within their boundaries (Lester et al., 2009; Molloy et al., 2009; Mosquera et al., 2000), but MPAs may also benefit adjacent fisheries through mechanisms such as adult and juvenile fish emigration ("spillover effect"; Rowley, 1994), or pelagic egg and larval exports (Harrison et al., 2012; Pelc et al., 2010, 2009). However, the magnitude of this biomass export from MPAs, its role in sustaining fisheries, and its composition are still poorly known.

Ecosystem modeling approaches can provide support for answering these questions. Among ecosystem models, Ecopath with Ecosim (Christensen et al., 2005; Christensen and Walters, 2004) has been applied numerous times to model MPAs and their trophic functioning (30 applications registered in EcoBase; Chapter 2). However, only a few of these models focused on the potential role of MPAs in sustaining fisheries (e.g., Le Quesne et al., 2008), their contribution at a larger scale (e.g., Mauritanian shelf; Guénette et al., 2014), and the potential export of fish biomass from the reserve (Valls et al., 2012).

Based on available case studies, the current analysis used trophodynamic modeling tools to investigate trophic functioning and the potential spillover effect of three different MPA ecosystems, which have been previously modeled using EwE. Two types of modeling approach were employed: (i) Ecopath (Christensen and Pauly, 1992; Polovina, 1984) to compare outcomes

(model derived indicators) of the three case studies and to estimate the fish biomass potential export (i.e. the potential spillover effect) from each MPA, and (ii) EcoTroph (Gascuel, 2005; Gascuel and Pauly, 2009) to derive additional indicators, to simulate the impact of hypothetical fisheries inside the MPAs, and to estimate the biomass of fish that could potentially be caught by these fisheries (i.e. catch losses). These estimates were compared to the potential exports for each reserve (i.e. the fish biomass not used in the trophic network and so possibly emigrating). Finally, the potential spillover effects were discussed, as well as possible improvements in the analysis of MPA efficiency.

4.3 Materials and methods

4.3.1 MPA case studies and Ecopath models

Three MPAs were investigated, for all of which Ecopath models have previously been built: two on the French Northwestern Mediterranean coast and one on the Senegalese coast (Figure 4.1). Available models and associated trophic spectra were used to analyze common features, especially regarding potential relative fishing impacts and biomass exports, in these three contrasting MPAs (Table 4.1):

- The Bonifacio Strait Natural Reserve was created in 1999. It covers approximately 800 km² and is characterized by a predominantly rocky substrate and *Posidonia oceanica* seagrass beds at shallow depths (Pluquet, 2006). Artisanal and recreational fishing activities are allowed in some parts of the MPA. The Ecopath model was originally developed by Albouy et al. (2010) for the years 2000-2001.

- The Port-Cros MPA is a small insular reserve created in 1963. The MPA has a total area of 12.9 km², 30% of which is covered by seagrass meadows. As in Bonifacio, small-scale fishing activities are permitted with specific restrictions in some parts of the MPA (Cadiou et al., 2009). The Ecopath model was originally developed by Valls et al. (2012) for the years 1998-2008.

- The Bolong de Bamboung is a small saline tributary of the Sine Saloum estuary. The MPA covers 6.8 km² including 4.7 km² of intertidal banks. The bolong has been monitored since 2003 (Albaret, 2003) and fishing has been prohibited since 2004. Two Ecopath models were developed for this site by Colléter et al. (2012): one for 2003, when fishing was still allowed, and one for the 2006-2008 period, after the establishment of the MPA. Given the context of this work, the latter was used.

Table 4.1 Characteristics of the three MPA case studies and their associated Ecopath models.

		Bonifacio Strait Natural Reserve	Port-Cros MPA	Bolong de Bamboung MPA
MPA characteristics	*Creation year*	1999	1963	2004
	Area (in km²)	800	12.9	6.8
	Fishing activities	Yes	Yes	No
Ecopath model	*Reference*	Albouy et al. (2010)	Valls et al. (2012)	Colléter et al. (2012)
	Modeled period	2000-2001	1998-2008	2006-2008
	Number of groups	32	41	31
	Biomasses estimated by Ecopath (in % of the total number of groups)	31	34	26
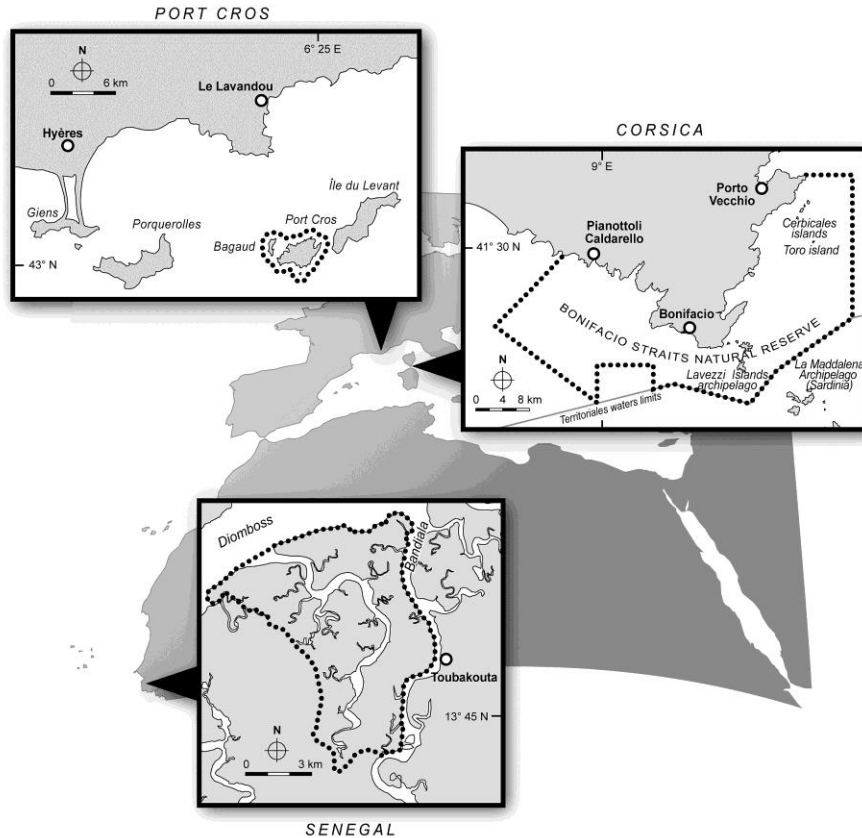
Figure 4.1 Location of the three MPAs: the Port-Cros National Park on the Mediterranean French coast, the Bonifacio Strait Natural Reserve in Corsica (France), and the Bolong de Bamboung in Senegal.

The three Ecopath models were developed within a French national program (ANR-Amphore) with the objectives of modeling trophic networks and assessing the effectiveness of MPAs. Their structure differed in order to properly reflect each ecosystem and its typical characteristics, but their construction satisfied common criteria (Table 4.1). These Ecopath models included all the biological ecosystem components using 32 trophic groups for Bonifacio, 41 for Port-Cros, and 31 for Bamboung. The ratio of the number of fish trophic groups to present fish species was in the same order of magnitude for the three models (21% for Port-Cros and Bonifacio, 25% for Bamboung). Mediterranean models were more detailed for invertebrate

compartments since more information was available. The input data (especially biomass estimates) for the models came mostly from field studies (see details in Albouy et al., 2010; Colléter et al., 2012; Valls et al., 2012). Biomasses estimated by EwE concerned 34% of the groups for Port-Cros, 31% for Bonifacio, and 26% for Bamboung. These biomasses referred almost exclusively to the secondary consumer groups, for which biomass estimations were rare. On the contrary, fish biomass estimations were of good quality, as they mostly came from field studies corresponding to the modeled periods (see Appendix E for parameter details).

The pre-existing models were homogenized by adjusting some of the model input parameters. The two kinds of initial Ecopath parameters that could be standardized without affecting the structure of the models were adapted (see Section 2.3 for a presentation of EwE core principles and equations): (i) The assimilation efficiency (U/Q), which is an estimate of the fraction of the food that is not assimilated (i.e. consisting of urine and feces) and directed to the detritus, was set to the same value for similar functional groups: 0.11 for carnivorous fishes, cephalopods and birds, 0.55 for herbivorous fishes, 0.4 for herbivorous zooplankton, 0.13 for macroplankton, 0.4 for echinoderms, 0.58 for polychaetes, 0.38 for gastropods, 0.27 for amphipods, 0.2 for decapods and other crustaceans, 0.6 for suspensivors, and 0.2 for other fishes by default (Christensen et al., 2005; Conover, 1966; Gaudy et al., 1991; Pandian and Marian, 1985a, 1985b; Pandian and Vivekanandan, 1985; Winberg, 1956); (ii) Ecotrophic efficiencies, which are the fractions of production used in the system, were set to 0.8 for all the invertebrates (secondary consumers) whose biomass was unknown, and to 0.6 for phytoplankton (see Table E.1, Table E.2, and Table E.3 for the parameter details). The first parameter U/Q has a default value of 0.2 for consumer groups in Ecopath (Christensen et al., 2005; Winberg, 1956). It influences the total amount of flows to detritus, and some derived ecosystem indices that were

analyzed (see Section 4.3.3). Contrary to the Bamboung and Port-Cros models, the Bonifacio model originally integrated more precise estimates for the different functional groups (see Albouy et al., 2010). Thus, this parameter was standardized. The second parameter, EE, constitutes an important parameter in Ecopath. Models were sometimes built with the aim of representing the minimal biomass of prey required to feed predators. By using an EE of 0.95 as input (for many groups in Polovina (1984) original model; based on Ricker (1968)), Ecopath solves the mass-balance equation (Eq. (2.1)). It calculates the biomass required for predator groups' consumption and catches, plus 5% corresponding to other mortality (1-EE). Consequently, a common representation of prey abundance was included, and EEs were set at similar values for functional groups whose biomasses were unknown (only low TL groups: primary producers and secondary consumers, no fish groups). This enabled uniform comparisons and simulations using ecosystem indices and EcoTroph (see below).

4.3.2   Use of the EcoTroph model

EcoTroph (ET), i.e., a modeling tool recently incorporated as a plug-in to EwE software (see Section 3.3 for a presentation of the EcoTroph model and its use), was also used to compare the homogenized Ecopath models and to estimate the fish biomass that could potentially be caught by fisheries (i.e. catch losses, see Section 4.3.4). Two ET routines (also available as R-functions; Appendix B) were used. ET-Transpose enables the conversion of data referring to functional groups (extracted from Ecopath) into data referring to trophic classes in order to create trophic spectra. These data represent the current distribution of biomass B_τ, production P_τ, catches Y_τ, fishing mortality F_τ ($F_\tau = Y_\tau/B_\tau$), or fishing loss rate ($\varphi_\tau = Y_\tau/P_\tau$) across TLs, and thus ecosystem characteristics can be compared. ET-Diagnosis is used to simulate the effect of

different fishery mortality scenarios on trophic spectra coming from ET-Transpose. Different effort multipliers are applied to the initial fishing mortalities. A null effort multiplier corresponds to a fishery closure (F=0), and allows users to rebuild an estimate of the unexploited status of the studied ecosystem. Flow equations (see Section 3.3) enable the calculation of biomasses, productions, and catches at the equilibrium for each trophic class and effort multiplier. Effects of fishery mortality changes at an ecosystem scale include biomass and kinetic changes but also impacts on the mean trophic levels of the catch and of the total biomass (Gascuel and Pauly, 2009).

ET-Diagnosis enabled to simulate various fishing mortalities, particularly catch losses induced by MPA enforcement (see Section 4.3.4). The last version of this routine was considered, estimating two distinct flow kinetics: one for the whole ecosystem biomass and one solely for the biomass accessible to fisheries (see Section 3.3) (Gascuel et al., 2011). Thus, simulations required setting up the accessibility to fishers of each trophic group in the Ecopath model, a parameter that has been theoretically defined as the proportion of a species or group that would be caught under the hypothesis of an infinite fishing effort (Gascuel and Pauly, 2009). This parameter takes into account whether a species is targeted by fisheries or not. Therefore a trophic group composed of a few target species and a lot of non-target species will have a lower accessibility than a group containing only targeted species. We considered that only fish groups were accessible to fisheries, removing invertebrate groups from originally targeted species (null values for invertebrates; see Table E.1, Table E.2, and Table E.3). This enabled a consistent comparison between simulated catch losses and potential biomass exports (see Section 4.3.4). Using this procedure, we derived an accessible biomass trophic spectrum along with a distinct

kinetic. This enabled the calculation of accessible biomass under different fishing mortality scenarios.

4.3.3   Ecopath and EcoTroph ecosystem indices analysis

Ecopath and ET enable the calculation of several ecosystem indices (Table 4.2), which provide insight into the structure and functioning of the simulated ecosystems. In particular, the EwE software includes a large number of ecological indicators based on trophic flows, thermodynamic concepts, information theory, and network analysis (Christensen and Walters, 2004; Coll et al., 2006). Four indicator categories were defined:

- Ecosystem characterization indices focused on the size of the ecosystem in terms of biomass and flow. Total biomass (TB) is the sum of all living biomass in the system (without detritus, in $t.km^{-2}$). Total system throughput (TST) is the sum of all flows in the system (in $t.km^{-2}.year^{-1}$). It represents the "size of the entire system in terms of flow" (Ulanowicz, 1986) and is an important parameter for comparison of flow networks (Christensen et al., 2005).

- Fisheries indices included the total catch (in $t.km^{-2}.year^{-1}$), and the primary production required for supporting this amount of catch, expressed as a ratio over the total primary production (PPR in %). This ratio is considered a measure of the overall impact of fishing on the entire ecosystem (Chassot et al., 2010; Pauly and Christensen, 1995; Swartz et al., 2010). The mean TL of the catch was also analyzed, as an indicator of the pattern of ecosystem exploitation (Pauly et al., 1998).

- Trophic biodiversity of the ecosystem can be estimated from ET outputs, using the mean TL of the biomass and accessible biomass (i.e. potentially harvested by fishers) (Pauly and Watson, 2005).

- Maturity indices are based on ratios. The ratio of total primary production to total respiration (TPP/TR) is expected to be different from 1 in immature or stressed environments, reflecting the fact that production normally exceeds respiration in the early phases of system development (i.e. TPP/TR>1), while the opposite occurs in stressed ecosystems (TPP/TR<1; Odum, 1971). Conversely, mature systems have a ratio approximating 1 (Odum, 1969). The ratio of total primary production to total biomass (TPP/TB) varies with the development status of the systems (Christensen and Pauly, 1993a). Developing systems tend to have a high TPP/TB, due to low biomass and high production values, while developed systems tend to have high biomass and low production rate values. The ratio of total biomass to total system throughput (TB/TST) is expected to be greatest at the most mature stage of a system (Odum, 1971). This ratio can take any positive value, and is expressed in years (Christensen et al., 2005). Finn's cycling index expresses the percentage of TST that is recycled (Finn, 1976). This is a measure of ecosystem complexity (Allesina and Ulanowicz, 2004), and can also be related to ecosystem maturity (Christensen and Pauly, 1993a). Finn's mean path length is defined as the average number of groups through which an inflow or outflow passes, i.e., the total number of trophic links divided by the number of pathways leading from preys to consumers (Christensen et al., 2005; Finn, 1980). This value is expected to increase with maturity (Christensen et al., 2005).

4.3.4   Assessing MPA effects and potential exports

Based on the homogenized Ecopath models, and using ET-Diagnosis, each MPA ecosystem was first modeled under a pristine hypothesis (F=0). This was applicable only to the Mediterranean MPA models since no catches were recorded in the Bamboung MPA Ecopath model (Appendix E; small fishing activities allowed in Mediterranean MPAs). Then, the impact of hypothetical new fisheries was simulated since the ones currently permitted corresponded to strictly regulated activities. Thus, for each unfished modeled ecosystem, the effect of different fishing scenarios was simulated based on logistic curves of the accessible biomass fishing mortality (F^*) function of the trophic level (Figure 4.2). Each curve was defined by a F^* asymptotic value experienced at high TLs conventionally ranging from 0 to 1 year^{-1}. It was also defined by the trophic level where F^* is equal to 50% of the asymptotic value, i.e. the TL at first catch, noted TL_{50} (which is analogous to the mean length at first capture; Beverton and Holt, 1957).
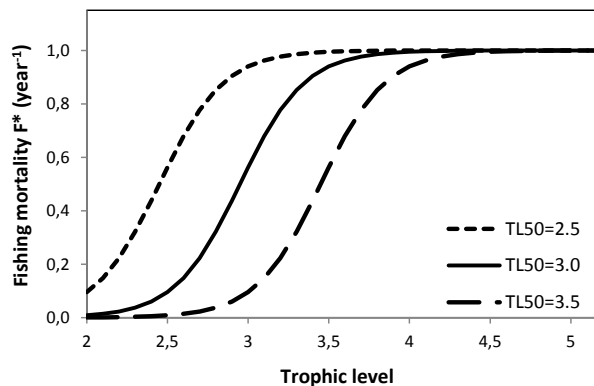
Figure 4.2 Hypothetical fishing scenarios based on logistic curves of the accessible biomass fishing mortality (F^*) function of the trophic level. Each curve was defined by a F^* asymptotic value experienced at high TLs conventionally ranging from 0 to 1 year^{-1} (here equal to 1.0), and by the trophic level at first catch (TL_{50} equal to 2.5, 3.0, and 3.5).

The reference scenario refers to a medium trophic level at first catch value equal to 3.0. Two extreme values were considered for sensitivity analyses: 2.5, which mimics a fishery where almost all accessible groups are targeted (as the fishing mortality is not null for low trophic levels comprised between 2 and 2.5), and 3.5 representing a fishery only targeting higher TL classes (i.e. predatory fishes). Each simulation was done with the standard EcoTroph parameterization (Appendix B; Colléter et al., 2013a). It referred to an equilibrium state and provided biomass, accessible biomass, production, catch, and fishing mortality trophic spectra for given F^* and TL_{50}. Finally, total catch, relative accessible biomass (compared to the pristine hypothesis), and mean trophic level of the biomass for the whole ecosystem were displayed as a function of F^*. This approach enabled to comparatively assess the resistance of MPA ecosystems to fishing as well as the effects of MPA enforcement. From a fishing perspective, a no-take MPA constitutes a particularly severe management tool since fishers are excluded from potentially lucrative fishing grounds. Thus, total catches that we estimated corresponded to catch losses, i.e. the fish biomass that could be caught by these hypothetical fisheries if no MPAs were implemented.

The last step of this analysis was to estimate the potential biomass that could be exported from each reserve, i.e. the potential spillover effect. The exports of fish biomass only were considered, since they would be directly valuable to the fisheries outside of the MPA. The method developed in the Port-Cros case study (Valls et al., 2012) was used; it is based on the assumption that fish productions that are not fully used in the ecosystem (either passed up the food web, used for biomass accumulation, or migration) are exportable. In the base homogenized Ecopath models, migrations and biomass accumulations were assumed to be equal to zero for all functional groups and the EEs were estimated by the model, especially for all fish groups. Here,

the three Ecopath models were modified by setting high ecotrophic efficiencies (EE=0.95) to all fish groups. By fixing ecotrophic efficiencies, the balance of the model was changed. As a standard feature, Ecopath then enabled to estimate net migration as the additional fraction of production not used in the system (assuming null biomass accumulations). Such an assumption implied that few fishes of these groups died for reasons other than predation, exploitation, or other natural mortalities (assuming that the latter is equal to 5% of the production of the group). Results were presented as export trophic spectra using the ET-Transpose routine to convert potential exports referring to functional groups into potential exports referring to trophic classes. Sensitivity tests were performed on the two main parameters that may affect such an estimate: the EE value using values equal to 0.90 and 1.00; and the import rate in diet matrices (i.e. the amount of food predated outside the MPA), to evaluate the sensitivity of the initial estimate of potential emigration to changes in predation pressure (increased by 10% for all fish groups in the sensitivity analysis).

4.4   Results

4.4.1   Analysis of trophic spectra

The different trophic spectra associated with the three Ecopath base models were computed. The biomass trophic spectra (Figure 4.3a) highlighted the difference in structure between the two North-western Mediterranean coastal ecosystems and the West African estuarine site. Mediterranean MPAs exhibited higher biomass (and production), especially for the high trophic classes. The Bonifacio ecosystem showed a higher biomass of forage fish (i.e. intermediate TLs, $2.7<TL<3$) compared to Port-Cros, but, compared to Bamboung, both

exhibited a high total biomass and a large abundance of predatory fishes (high TLs). The slope of the biomass trophic spectrum was steeper for Bamboung, which reveals slower transfers in the food web and smaller trophic efficiencies than in the two Mediterranean protected areas. The accessible part of the biomass (Figure 4.3b) also exhibited greater values for the high trophic classes in the two Mediterranean MPAs compared to the Bamboung, with the highest accessible biomass in Bonifacio (23.0 t.km^{-2} in total for TLs$\geq$3.3, 13.0 in Port-Cros, and 2.5 in Bamboung). However, accessible biomass was higher for low TLs in Bamboung (2.3$\leq$TL$\leq$2.5). The Port-Cros case study had high accessible biomass for TLs around 2 due to Salema (*Sarpa salpa*), as the Bamboung case study, to a lesser extent, due to the Tilapias. Accessible biomasses were close to zero for TL classes between 2.1 and 2.3 in Bamboung (2.1 and 2.5 in the two Mediterranean MPAs) since these TL ranges corresponded to invertebrate compartments. This highlighted differences in ecosystem structure between the Mediterranean MPAs and Bamboung MPA, and also in targeted trophic components among the three case studies.

The catch and fishing mortality trophic spectra (Figure 4.3c and Figure 4.3d) revealed a low degree of the allowed fishing activities in the two coastal Mediterranean MPAs. The catch spectra had similar general patterns at both sites. However, the lower TL classes (2<TL<2.2) were only exploited in Port-Cros. The resulting fishing mortality was about 0.01 year^{-1} for high TLs and even lower for intermediate TLs. Such low fishing mortalities indicated that small-scale fishing activities should have a negligible impact at the ecosystem scale. No catches were made in the Bamboung MPA, which explained the null fishing mortalities.
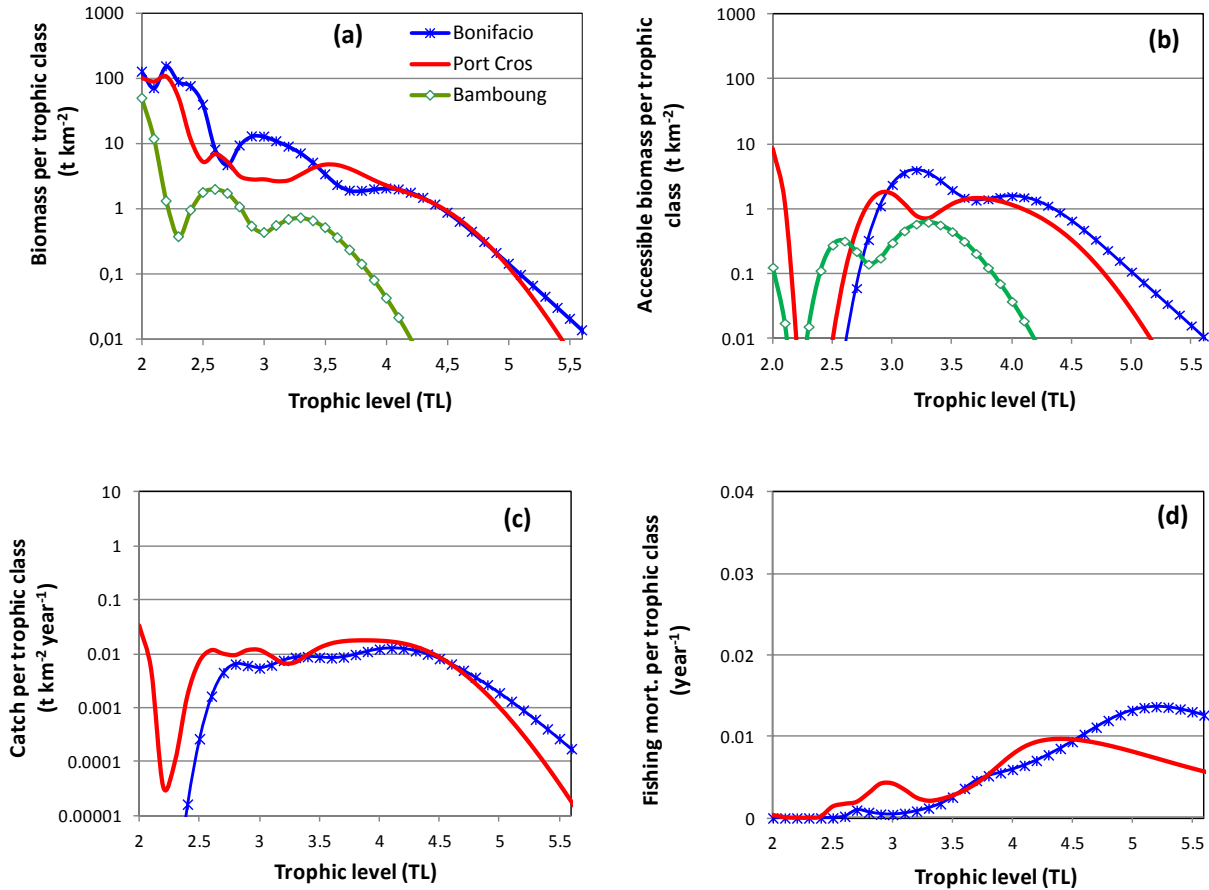
Figure 4.3 Trophic spectra for the three modeled ecosystems (Bonifacio, Port-Cros, and Bamboung): (a) distribution of the ecosystem biomass, (b) accessible biomass, (c) catch and (d) fishing mortality per trophic class.

4.4.2   Ecopath and EcoTroph ecosystem indices

The analysis of ecosystem indices emphasized the difference in structure between MPAs (Table 4.2). Ecosystem total biomass (TB) was much higher in the Mediterranean MPAs than in Bamboung. This was partly due to the high biomass of primary producers in the two Mediterranean ecosystems, and especially to the large *P. oceanica* biomass. However, this seagrass only feeds a few groups (*S. salpa*, echinoderms, gastropods) and does not constitute a major food source for the trophic webs under study (Vizzini and Mazzola, 2003). The biomass of

secondary producers (TL=2) was in the same order of magnitude in the three ecosystems, while biomass for higher TLs was again higher in the Mediterranean systems (Figure 4.3a). Thus, the low TB observed in Bamboung also resulted from low fish biomass related to the low trophic efficiency in this ecosystem (Colléter et al., 2012).

Table 4.2 Selection of Ecopath and EcoTroph system and network indices.

Parameter	Units	Bamboung	Port-Cros	Bonifacio
Total biomass (excluding detritus) (TB)	t.km^{-2}	107	2683	1820
Total biomass (excluding detritus+primary production)	t.km^{-2}	75	430	655
Total system throughput (TST)	t.km^{-2}.year^{-1}	4644	26457	32644
Total catches (Y)	t.km^{-2}.year^{-1}	0	0.32	0.19
Primary Production Required (PPR harvested groups/ Total primary production)	%	0	1.7	0.7
Mean trophic level of the catch (TL$_C$)	--	--	3.47	3.85
Mean trophic level of biomass (TL$_B$)	--	2.17	2.33	2.36
Mean trophic level of accessible biomass (TL$_{B*}$)	--	3.15	3.05	3.58
Total primary production/Total respiration (TPP/TR)	--	2.69	1.92	1.41
Total primary production/Total biomass (TPP/TB)	--	14.98	3.2	3.1
Total biomass/Total system throughput (TB/TST)	--	0.02	0.1	0.06
Finn's cycling index (FCI)	% of TST	7.9	9.3	13.12
Finn's mean path length (FMPL)	--	2.9	3.1	3.51

The total catch (Y) and the associated primary production required to sustain the fishery (PPR) had low values in the Mediterranean MPAs. The low PPR values indicated very limited fishing activities (less than 2%; see Chassot et al., 2010; Pauly and Christensen, 1995). The mean trophic level of biomass (TL$_B$) was lower in Bamboung than in Port-Cros and Bonifacio, where high-trophic-level fishes were more abundant. The mean trophic level of accessible biomass (TL$_{B*}$) was the highest in Bonifacio, where accessible biomass concentrated on predatory fishes (TLs≥3.3) covered 66% of the predator biomass. Port-Cros exhibited the lowest TL$_{B*}$ because of

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important accessible biomass for TLs around 2 and a lower coverage of predator biomass (33%). Bamboung had a slightly higher value than Port-Cros since accessible predator biomass represented 88% of predator biomass.

Almost all ecosystem indices describing the structure and dimension of the flows were higher in the Bonifacio and Port-Cros ecosystems than in Bamboung. As hypothesized by Ulanowicz (1980), the autocatalytic process tends to increase overall total system throughput (TST, sum of all flows, see Section 4.3.3), efficiency, and organization in the absence of major perturbations. Thus, the two Mediterranean MPAs logically appeared to be more organized with complex trophic networks generating important flows compared to the Bamboung.

The three maturity indices based on ratios of various ecosystem metrics (TPP/TR, TPP/TB and TB/TST) also showed the higher maturity of the Mediterranean MPA ecosystems. Based on Finn's cycling index (Finn, 1976), the ecosystem complexity of the sites was ordered as follows: Bamboung<Port-Cros<Bonifacio. The last two ecosystems showed considerable cycling through detritus, therein revealing a greater dependency on detritus-related processes than Bamboung. This recycling of nutrients tends to enhance stability and increase an ecosystem's ability to recover from perturbations (Vasconcellos et al., 1997). Finn's mean path length was also higher for the Mediterranean MPAs, which confirmed that these are more organized and complex trophic networks.

4.4.3   Resistance to fishery impact

Unsurprisingly, simulating a fishery inside each MPA resulted in a substantial degree of catch potential (see Figure 4.4). Simulations showed that the magnitude of this hypothetical catch highly depended on MPA case studies and on which trophic level classes would have been

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targeted (Figure 4.4 top). Based on the reference scenario ($TL_{50}=3$) and an accessible biomass fishing mortality (F^*) equal to 0.5, the potential catch was around 8.0 t.km⁻².year⁻¹ for Bonifacio, 4.4 t.km⁻².year⁻¹ for Port-Cros, with the Bamboung MPA exhibiting much lower potential yields (0.8 t.km⁻².year⁻¹).

These estimates appeared to be sensitive to the ecosystem fishing pattern. The Port-Cros and Bamboung case studies exhibited higher potential catches when reducing TL_{50} to 2.5, since this targets a much broader part of the ecosystem (4.9 and 1.0 t.km⁻².year⁻¹ for Port-Cros and Bamboung respectively). This showed the importance of potential yields from intermediate trophic levels. Conversely, Bonifacio had slightly lower potential catches (7.8 t.km⁻².year⁻¹) due to an accessible biomass concentrated on TLs≥3, thus enduring important accessible biomass fishing mortalities with a lower TL_{50} (and reaching a plateau for high F^*). Assuming that the fishery is targeting only predatory fishes (TL at first catch equal to 3.5) led to lower simulated catches: around 5.9 t.km⁻².year⁻¹ for Bonifacio, 3.4 t.km⁻².year⁻¹ for Port-Cros, and 0.5 t.km⁻².year⁻¹ for Bamboung. In this case, catches as a function of F^* followed a steeper growing curve since ecosystems were overall less impacted by the fishery.
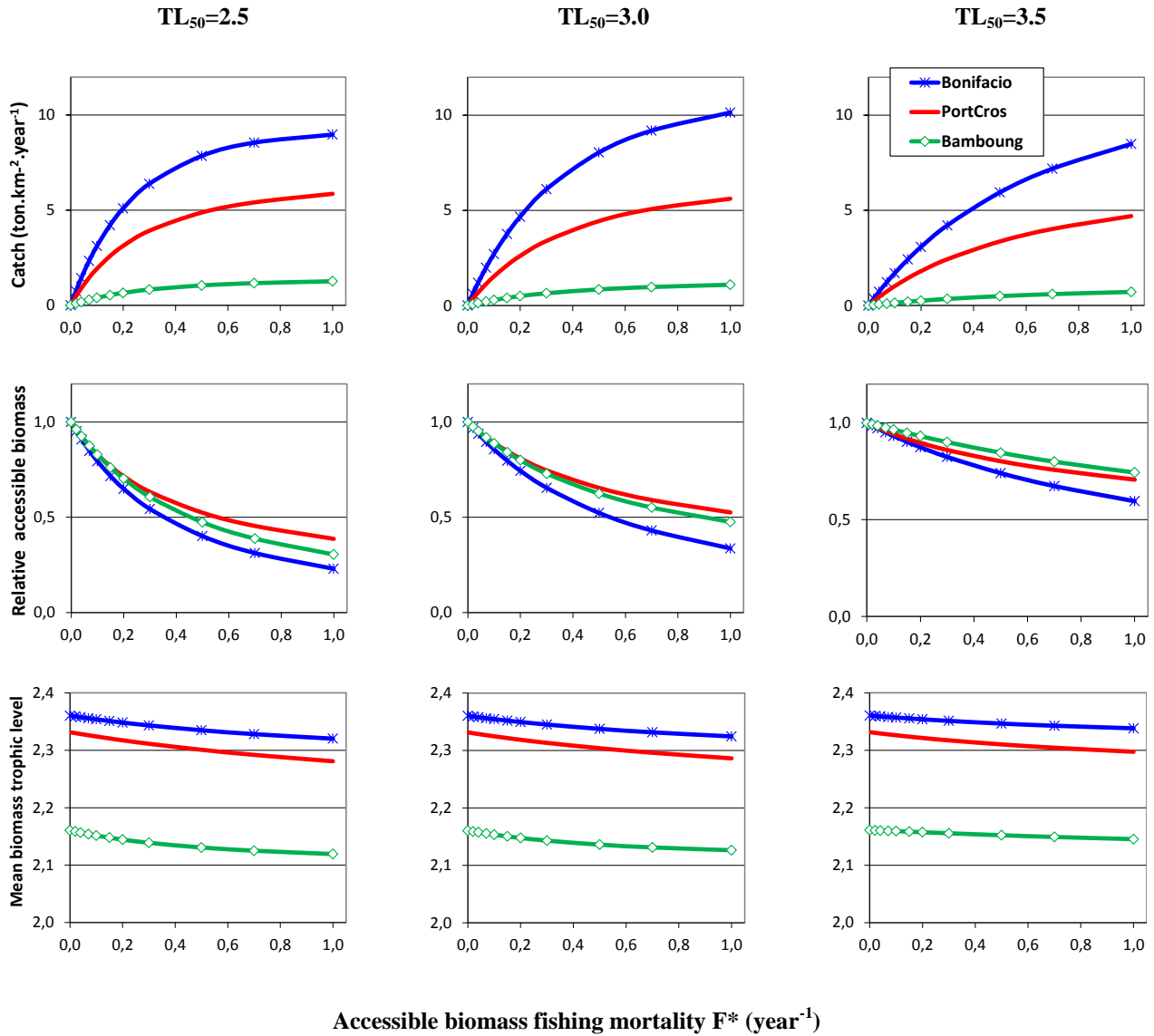
Figure 4.4 Simulation of hypothetical fisheries inside each MPA. Value of the catch (top), relative accessible biomass (conventionally set equal to 1 for $F^*=0$ year^{-1}) (middle), and mean trophic level of biomass (TL$_B$, bottom), according to the accessible biomass fishing mortality (F^*) used in the simulation. Central column refers to the reference fishing scenario simulating a trophic level at first catch (TL$_{50}$) equal to 3.0. Left and right columns present sensitivity analyses, mimicking a fishery targeting either a broader range of the ecosystem or predatory fish only (i.e. TL$_{50}$ equal to 2.5 and 3.5 respectively).

Compared to simulated fishing situations, MPA implementation ($F^*=0$) induced an increase in the ecosystem biomass, especially for the part that was accessible to fisheries (i.e. accessible biomass, Figure 4.4 middle). Based on the reference fishing scenario ($TL_{50}=3.0$), a 1.6-fold increase in the accessible biomass was observed from simulated $F^*=0.5$ to the closure of the fishery ($F^*=0$) for Port-Cros and Bamboung, and a 2-fold increase for Bonifacio. Induced increases were higher with a lower TL at first catch (2 to 2.5-fold increase in the accessible biomass), as the associated fishing scenario targeted almost all accessible biomass (see Figure 4.3b). On the contrary, MPA implementation had a lower impact if only higher TL classes were previously targeted ($TL_{50}=3.5$). Overall, the Bonifacio case study had a lower resistance to fishing impacts since its accessible biomass represented an important proportion of total biomass (see Section 4.4.2), and concentrated on TLs higher than 3.0. The common patterns observed in Port-Cros and Bamboung suggested an equivalent resistance to fisheries for the two MPAs.

Finally, MPA implementation resulted in an increase in the mean TL of the total biomass (Figure 4.4 bottom). Based on the fishing reference scenario, an increase of around 0.02 in the mean TL was observed from simulated $F^*=0.5$ to the closure of the fishery ($F^*=0$). This increase was at the same order of magnitude for all the ecosystems. The largest increase in mean TL (about 0.05) was obtained with a fishery that targeted a broad part of the ecosystem with a high accessible biomass fishing mortality (i.e. $TL_{50}=2.5$ and $F^*=1.0$). A higher TL at first catch resulted in a smaller increase since such exploitation had a lower impact on the whole ecosystem. High trophic levels were more sensitive to fishery impacts as the mean biomass trophic level decreased with an increasing F^*, which showed a greater relative impact on predators.

4.4.4   Estimation of the potential exports

Results on potential fish exports were demonstrated using potential export trophic spectra (Figure 4.5). The potential exports of the two Mediterranean MPAs showed relatively common patterns with a predominance of high TLs. Predatory fishes had high biomass with no or low fishing and predation mortalities (low EEs), thus enabling high potential exports. On the contrary, intermediate TLs were generally preyed upon more, thus limiting their potential exports. However, the Port-Cros MPA also exhibited high potential exports for species with a TL near 2, notably due to the high biomass of Salema (*S. salpa*), an abundant herbivorous fish in the system that is rarely preyed upon. Since the biomass of predatory fishes remained low, the Bamboung MPA showed lower potential exports for the high TLs. Intermediate TLs showed higher potential exports because of their important biomass and moderate predation mortality.

The Bamboung MPA had the lowest potential exports, with a total of 1.0 t.km^{-2}.year^{-1}, of which 0.8 t.km^{-2}.year^{-1} was accessible to fisheries. This estimate was at the same order of magnitude as the simulated catch loss due to the MPA implementation, under the reference scenario (around 0.8 t.km^{-2}.year^{-1} for F*=0.5 and TL$_{50}$=3.0, see Section 4.4.3). Thus, potential exports appeared slightly higher or lower than simulated catch losses, depending on which trophic level at first catch was used. The Bonifacio MPA also exhibited limited potential exports with a total amount of 2.6 t.km^{-2}.year^{-1}; 2.0 t.km^{-2}.year^{-1} was accessible to fisheries. This estimate appeared lower compared to the simulated catch losses (from 6.9 to 8.0 t.km^{-2}.year^{-1}, depending on the trophic level at first catch). On the contrary, the Port-Cros MPA exhibited higher potential exports, 8.1 t.km^{-2}.year^{-1}, of which 5.7 t.km^{-2}.year^{-1} was accessible to fisheries. This estimate was higher than the simulated catch losses for all fishing scenarios (with F*=0.5).

Based on the reference scenario, potential exports of accessible biomass outside the MPA exceeded catch losses induced by the closure of the fishery inside the MPA by about 30%.

Thus, biomass exports from the two small size MPAs appeared to counterbalance losses in potential fishery yields inside the MPA. Simulations showed that the increase in catch outside might be higher than if catches do occur in the Port-Cros ecosystem; in Bonifacio the catch opportunities inside the MPA appeared higher than the potential exports, even for moderate fishing pressures. In terms of absolute values, the total export from each MPA was highly dependent on its size. Thus, due at least in part to its small size (5 km²), Bamboung exhibited the lowest export value of about 5 t.year^{-1}, while biomass exports from the Port-Cros MPA (13 km²) were estimated at approximately 100 t.year^{-1}. In contrast, Bonifacio, which covers 800 km², had potential exports of around 2000 t.year^{-1}.
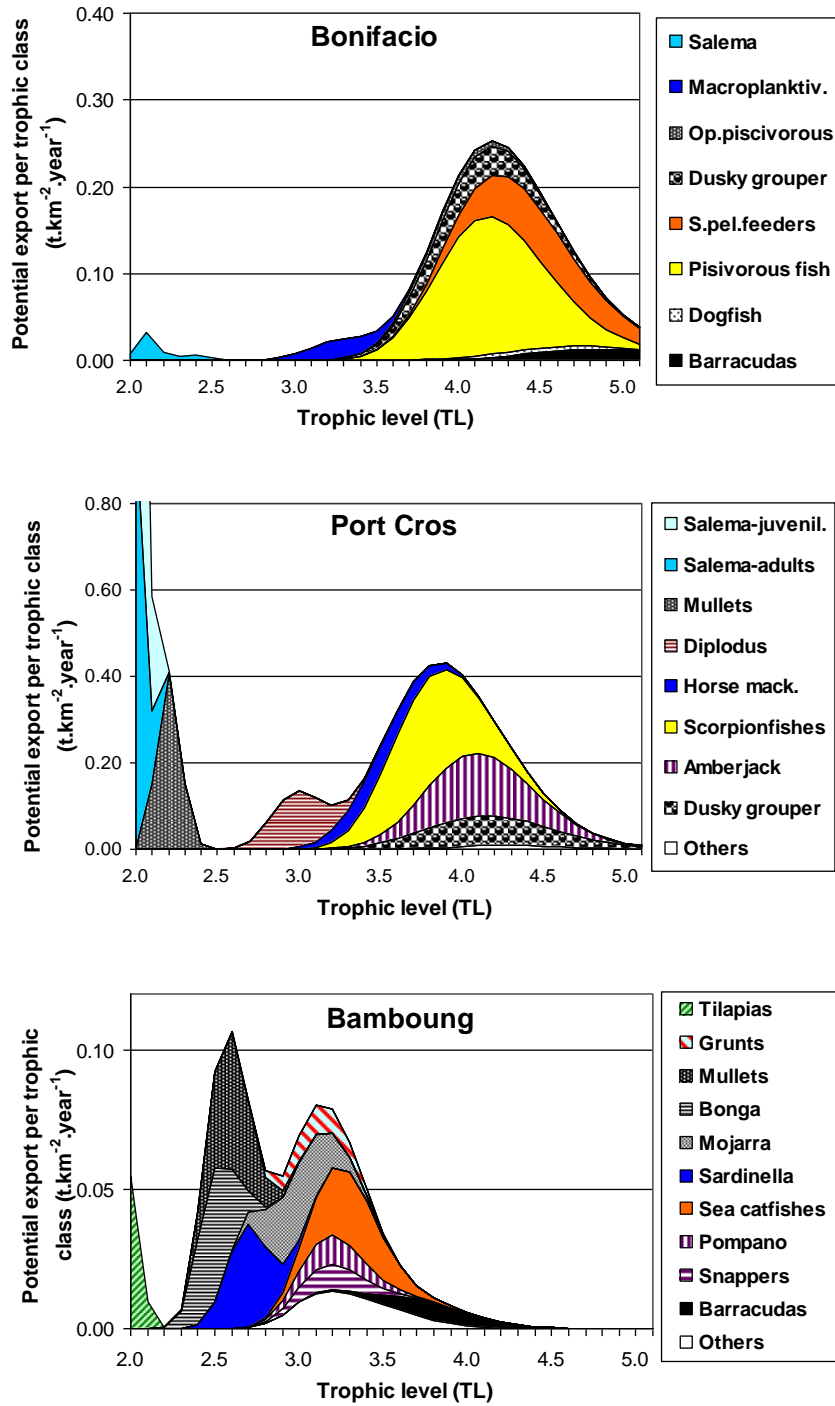
Figure 4.5 Estimates of the three MPAs' yearly potential exports (in t.km^{-2}.year^{-1}), i.e., net migration as the additional fraction of production not used in the system (assuming null biomass accumulations).
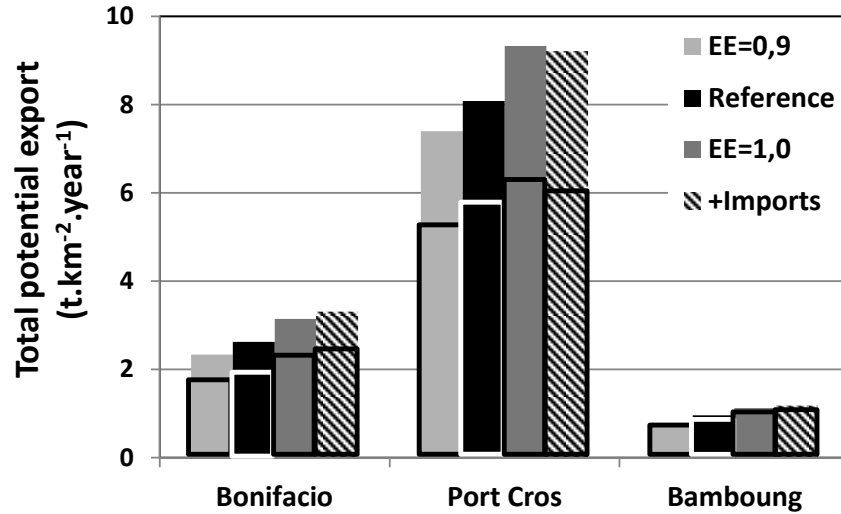
Figure 4.6 Sensitivity analysis of potential fish export estimates to the main Ecopath parameters used in simulations (boxed portions for accessible part): ecotrophic efficiencies (EE) of fish and part of imports in the fish diet.

Sensitivity analyses showed that the results were robust to the assumptions made on the Ecopath parameters with the highest impact (Figure 4.6). Variations in the value of ecotrophic efficiencies (EE) or additional imports of 10% in the diet of all fish changed estimated potential exports by up to 25%. However, conclusions drawn from the comparison between the potential exports outside the MPAs and simulated catches that could have been harvested inside the MPAs remained unchanged.

4.5   Discussion

4.5.1   New insights into the functioning and benefits of MPAs

This analysis of Mediterranean and West African estuarine MPA models enabled a better understanding of the existing differences in the trophic structure and functioning. For example,

the Bamboung MPA had a lower transfer efficiency reflected by the steep slope of the biomass trophic spectrum, low biomass, mean path length, and mean trophic level (TL_B). This was not surprising since the tropical estuarine situation of this MPA exhibits a typical ecosystem functioning similar to what has been suggested by previous studies (fish biomass, Baird and Ulanowicz, 1993; Finn's mean path length, Rueda and Defeo, 2003). Several ecosystem indices used in this analysis are dependent on model complexity and parameterization (Christensen et al., 2005). However, all indices indicated the same pattern, thus highlighting the structural differences between ecosystems and suggesting that Mediterranean coastal MPAs were more mature with higher biomass and flows than the estuarine Bamboung ecosystem.

The Mediterranean MPAs exhibited more complex trophic networks and greater trophic efficiencies. In comparison, the trophic network in Bamboung is not based on phytoplankton flows; instead it relies predominantly on the detritivores inhabiting this muddy ecosystem (Albaret, 2003). These conclusions seem logical considering the impact of environmental variations in this estuarine location that has important tide movement, and turbid waters, and is functionally different from the two Mediterranean MPAs. This could also be related to the duration of protection between the MPAs: 2 years after MPA enforcement for Bonifacio, 4 years for Bamboung, and 35 years for Port-Cros. However, differences between Bamboung and the two Mediterranean MPAs were more important than the differences between the two Mediterranean MPAs, due to a greater impact of the ecosystem type than the period of protection.

Despite the differences among MPAs, common features were found in the simulated effects of the MPAs. Results showed similar patterns of resistance to fishing with increases in relative accessible biomass and mean biomass trophic level for a decreasing fishing mortality.

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They were at the same order of magnitude for Port-Cros and Bamboung, with the Bonifacio ecosystem being slightly less resistant to the impacts of fishing. This result was consistent with the results of several synthetic studies on MPAs, which show an increase in the biomass and density of fish populations (e.g., Lester et al., 2009; Molloy et al., 2009; Mosquera et al., 2000). The increase in the mean TL emphasized the applicability of the MPAs as a conservation tool for large predatory fishes (e.g., Edgar and Stuart-Smith, 2009), which are more vulnerable (Gascuel et al., 2008; Pauly et al., 1998) and often mainly targeted by fisheries. Protection from fishing allows these species to attain larger sizes and abundances resulting in their greater proportional contribution to fish biomass in MPAs (Micheli et al., 2004). Results obtained from the Bamboung MPA prior to its enforcement (Colléter et al., 2012) also showed that the closure of the fishery led to a slight increase in the mean trophic level of the ecosystem biomass (TL_B=2.16 in 2003, 2.17 in 2007) and to a larger increase for the accessible biomass (TL_{B*}=2.63 in 2003, 2.91 in 2007). This indicated a shift in the Bamboung trophic network with an increase in the biomass of predatory fishes (high TLs) previously impacted by fisheries. Thus, the three MPAs fulfilled their role in terms of biodiversity conservation and the protection of targeted species.

Despite the fact that no-take MPAs prohibit fishing activity within their boundaries, there have been several indications that MPAs may act as sources of exploitable fish through "spillover" into the surrounding environment (Gell and Roberts, 2003; Goni et al., 2008; McClanahan and Mangi, 2000; Russ et al., 2003). However, these studies focused on the catches made by artisanal fisheries around MPAs, on specific species or using specific gears, and showed an increase near the boundaries and a declining gradient in catch corresponding to the distance from the protected zone (effect on 100s of meters calculated by Abesamis et al., 2006; Harmelin-Vivien et al., 2008; Russ et al., 2003). Furthermore, persistence and harvests of biomass exports

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across MPA boundaries have been shown to be greatly reduced by the redistribution of fishing effort from reserves to neighboring fishing areas and fishing along reserve borders (Grüss et al., 2011b). Here, using food web models, it was possible to estimate potential exports of exploitable fishes and compare them with the catch losses at the ecosystem scale. Results suggested that the total potential export is quite weak, especially for small and isolated MPAs (Bamboung and Port-Cros), but it may exceed the loss in potential fishery yields, especially when only high TLs were previously targeted inside the MPAs. On the contrary, the total potential exports were higher at Bonifacio due to its large area (2000 t.year^{-1} for 800 km²), but remained too low to offset potential yields.

The location, size and characteristics of the protected ecosystem are important parameters to take into account when MPA objectives are fishery-related, as they can lead not only to fishery benefits but also reductions in overall yield (Le Quesne et al., 2008; Mesnildrey et al., 2013). Benefits for fisheries were reported in several case studies: Roberts et al. (2001) found that catch per unit of effort (CPUE) of fish traps increased by 46 to 90% in 5 years around a network of reserves in St-Lucia, Galal et al. (2002) found that CPUE of the trammel net fishery increased by 66% in 5 years in Nabq (Egypt), and Goni et al. (2010) found that harvested spillover of lobsters offset the loss of yield resulting from the reduction of fishing grounds set aside in the Columbretes Islands marine reserve, producing a mean annual net benefit of 10% of the catch in weight. Other studies reported higher increases in CPUE (Maypa et al., 2002; Tawake et al., 2001). In this analysis, these gains depended on the fishery scenarios; a lower TL at first catch reducing them and even leading to losses for the Bamboung and Bonifacio case studies (TL$_{50}$=2.5). Conversely, some studies suggest also that the spillover effect can be weak (Davidson, 2001). The three case studies had different characteristics regarding the year of

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protection, the size, the ecosystem type, and the regulations. Results obtained call for an analysis at a larger scale including other case studies to better understand which parameters influence the spillover effect at the ecosystem scale. It has been shown that both the age and the size of marine reserves impact their efficiency (Babcock et al., 2010; Claudet et al., 2008; Vandeperre et al., 2011), yet other key features, such as enforcement (Guidetti et al., 2008), regulation, and degree of isolation (Edgar et al., 2014) also have an impact on their success.

Results suggest that MPAs are especially beneficial, in terms of catch potential, for fisheries that target high trophic levels. It also suggests that MPAs would be more beneficial in mature ecosystems, after a long period of protection, such as the Port-Cros MPA. It is characterized by a high biodiversity, a large biomass of predators and strong competitions, especially between intermediate trophic levels. Moreover, MPAs are usually implemented first for conservation purposes. Results confirm that such conservation objectives may be fulfilled without inducing catch losses, but simultaneously improving the catch potential of the surrounding environment. Here, the focus was put on trophic functioning and fishery-related MPA benefits. Non-monetary benefits of MPAs were not considered, such as cultural or education benefits and other ecosystem services (see Angulo-Valdés and Hatcher, 2010). It would be interesting to weigh the economic returns in terms of commercial catches against other non-fishery benefits (e.g., non-consumptive recreation activities as scuba diving or ecotourism). However, these analyses focusing on economic tradeoffs measures do not give the full picture of MPA benefits since they do not consider social or environmental benefits (Angulo-Valdés and Hatcher, 2010). Ecosystem models such as EwE and ET can provide diagnosis and indicators for assessing conservation and fishery-related effects of MPAs (Pelletier et al., 2008). However, they constitute only one way to look at MPA effects.

4.5.2 Using Ecopath and EcoTroph to assess MPA effects

A new way of looking at MPA efficiency was explored through the use of food web models and trophic spectra. Ecopath and EcoTroph appeared to be efficient tools for highlighting differences between ecosystem characteristics and functioning, and brought forth new insights into the discussion regarding MPAs. MPAs have been studied in depth, but too few studies question their real impact on trophic functioning and sustaining fisheries (e.g., Garcia et al., 2013; Gell and Roberts, 2003; Goni et al., 2010; Le Quesne et al., 2008; McClanahan and Mangi, 2000). Several Ecopath models have been developed on MPA case studies to explore the impact of this management tool on the underlying ecosystem trophic network (e.g., Albouy et al., 2010; Colléter et al., 2012; Le Quesne et al., 2008; Valls et al., 2012). Furthermore, the EcoTroph model constitutes a uniform framework for these models and enables their comparison using trophic metrics. The use of trophic spectra is of great interest as they furnish a simple representation of complex ecosystems and fishery impacts (Gascuel et al., 2005; Rombouts et al., 2013).

The calculation of potential exports from the MPAs used in this chapter constitutes a first and simple estimation of this process. Only potential fish catches and exports were considered, and it did not account for invertebrate groups that can also lead to harvested spillover (e.g., Goni et al., 2010). This was necessary since Ecopath models were less precise regarding input parameters of invertebrate groups (i.e., several biomasses estimated by the model), and no data (as biomass estimates and habitat mapping) were available to perform a rigorous analysis. Then, Ecopath models establish a mean ecosystem representation across time (at least one year), and the movement mechanisms are not explicitly accounted for (biomass estimates represent a mean value over the year). Here, it was assumed that almost all fish production not used in the trophic

network (through predation and other forms of natural mortality) was potentially exportable. In fact, EE values are heavily dependent on the construction and parameterization of the model, and also depend upon how the ecosystem is represented (Christensen et al., 2005). However, the sensitivity analyses showed that the conclusions were robust to variations in the EE value setting, and changes in the diet import rates. More importantly, potential exports were quantified using the standard Ecopath procedure based on linear algebraic equations, implying an assumption of linear effects of mortality and biomass changes, and thus neglecting density-dependent effects (typically nonlinear) that exist in food webs (Walters et al., 2000). In fact, the biomass accumulation that occurs within MPA boundaries is likely to lead to density-dependent spillover, which may take years or decades to develop (Abesamis and Russ, 2005; Russ and Alcala, 2004). Furthermore, intermediate-sized prey species are more likely to cross MPA boundaries than are larger individuals because of interactions with conspecifics and predation risk (Abesamis and Russ, 2005; Shepherd et al., 2010).

Specific density-independent mechanisms of adult and juvenile movement (Grüss et al., 2011a) were not explicitly considered: the home range of the animal, nomadism, and different migration types. The impact of habitat and localization should also be considered as these factors can impact the potential exports. For example, when habitats within MPAs are more favorable than outside, spillover may be negligible or slower (e.g., Freeman et al., 2009; Lowe et al., 2003). In contrast, when habitats are suitable and homogeneous across MPA boundaries, movement may be encouraged (Tupper, 2007). From this viewpoint, spill-over assessments could have been better estimated using dynamic and spatial models (e.g., Ecosim and Ecospace), which can further account for potential exports also in relation to density outside MPA and spatial components. But no data, and especially no time series, were available to fit such a model

in this analysis. Therefore, the approach used in this chapter should be considered as a first step in using food web models to assess the effects of MPAs, and future works incorporating more case studies and possible complex processes (density-dependent and independent) should be encouraged to better analyze and assess spillover and fishery benefits at a large scale.

In conclusion, the objective of managing fish stocks often includes the need to plan over large spatial and time scales. The magnitude of estimated potential exports is related to the size of the MPA: the smaller the MPA, the smaller the magnitude of its exports. This insight suggests the need for MPA networks and/or sufficiently large MPAs to effectively protect juveniles and adults and provide important exports (e.g., Gell and Roberts, 2003; Le Quesne and Codling, 2009; Mesnildrey et al., 2013; Moffitt et al., 2009). Indeed, the potential exports from small and/or isolated MPAs may only be enough to sustain artisanal fisheries in fishing grounds very close to MPA boundaries. Notwithstanding the fact that such activities might be of high cultural and social significance, this analysis indicates that further research is needed to improve MPA effects and associated fisheries management at a larger scale (Sale et al., 2005; Willis et al., 2003).

Finally, results did not account for egg and larval exports, both of which can make a significant contribution to the replenishment of populations in both protected and fished areas (Pelc et al., 2010, 2009; Planes et al., 2009). The redistribution of fishing effort does not affect the dispersion of larvae and eggs (Grüss et al., 2011b), and important benefits could potentially be reaped from these exports compared to exploitable biomass exports by the MPA (Harrison et al., 2012). Apostolaki et al. (2002) found in a modeling study that the greatest fishery benefits were obtained by establishing marine reserves both in spawning and nursery areas showing the importance of the pre-recruitment stages and habitat protection. Considering results obtained in

this chapter, the possible benefits of designing a MPA to focus on the production of exploitable biomass (by 'trophic production') seem to be scarce for stock management. By contrast, MPA management that aims to enhance fish stocks and fishery yields at a larger scale calls for more studies on habitat specificities, egg/larva production, export and dispersal, and ecosystem connections (Fox et al., 2012).

Chapter 5: A meta-analysis of Ecopath models published worldwide using Ecotroph, identification of typical trophic functioning in marine ecosystems

5.1 Summary

A great number of Ecopath models have been developed worldwide to represent and study marine ecosystems' food webs. EcoTroph enables the construction of a unique framework to compare these Ecopath models, the trophic spectrum. Thus, a meta-analysis based on 127 Ecopath models representing marine ecosystems was performed to identify typical trophic functioning. EcoTroph was used to simulate all the models at an unexploited state and to compute the associated biomass, production, and kinetic trophic spectra. Trophic spectra variability was analyzed considering two traits: the ecosystem type, and the latitude. First, a principal component analysis (PCA) was performed to apprehend biomass trophic spectra variability and explore the correlation structure between the different TL classes. Then, linear models were adjusted to statistically assess the differences among ecosystem types and compute mean trophic spectra by ecosystem type. Finally, several trophic indices were extracted from each ecosystem trophic spectrum and compared. Results indicated that typical trophic functioning can be identified based on their biomass trophic spectra. It notably showed that 'lagoon' ecosystems were characterized by low biomass at high trophic levels and low net transfer efficiencies. On the contrary, 'upwelling' ecosystems were characterized by high net transfer efficiencies and biomasses at high trophic levels. Overall, ecosystem types were distinguished by different biomass and associated trophic indices, these differences being mainly driven by different production, but also kinetic for some ecosystem types.

5.2 Introduction

A food web describes the trophic interactions between ecosystem components, i.e. the flows of energy and matter within an ecosystem. These trophic interactions consist of processes that determine ecosystem structure and functioning, but also the response to both internal and external disturbances. In fact, predator-prey interactions are important regulators of the ecosystem functioning (see Chapter 3; Allesina and Pascual, 2008; Walters and Martell, 2004). However, fishing ecosystem effects are still unaccounted for by a predominant use of single-species assessments in fisheries regulation (Jennings and Kaiser, 1998). The move toward an EAF calls for a better understanding of marine ecosystems' trophic functioning and the related environmental and fishing impacts to answer queries by management stakeholders. Quantitative analyses on marine ecosystems' trophic functioning are still lacking, especially regarding its variability through ecosystems. Trophic processes taking place in aquatic ecosystems have been explored and defined since several decades, thanks notably to the development of the trophic level concept (see Section 1.4, and Eq. (2.3)) (Elton, 1927; Lindeman, 1942; Odum and Heald, 1975). However, trophodynamic analyses started to be widely applied to marine ecosystems since the begin of the 1980s only (see a review in Libralato et al., 2014). An important step towards a better understanding of marine ecosystems' trophic functioning was the development of ecosystem models, such as Ecopath with Ecosim (Christensen and Pauly, 1992; Christensen and Walters, 2004; Polovina, 1984), OSMOSE (Shin and Cury, 2004, 2001), size spectra (Jennings et al., 2008), Atlantis (Fulton et al., 2011), or Linear Inverse Model (LIM; Niquil et al., 2011; Vézina and Piatt, 1988), that have been applied to an increasing number of marine ecosystems. Ecosystem modeling is an important tool for the evaluation of scenarios and trade-

offs, and to explore further the trophic functioning of marine ecosystems (Plagányi, 2007). It is nowadays an active field of research with an approximately 20% growth rate per year in the annual number of model publications since 1995. More than a half of these publications are related to the EwE modeling approach (Christensen and Walters, 2011).

EwE model was applied on hundreds of case studies covering a wide diversity of ecosystems type and size (see Section 2.5). EwE also contributed in a major way to the reemergence of the trophic level concept, especially as TLs were not an input to EwE, but an estimated parameter resulting from the species' diets (see details in Section 2.3). Furthermore, this modeling approach enables the calculation of ecological network indices (Lindeman, 1942; Odum, 1969; Ulanowicz, 1980), that enable to quantify structural and functional properties of food webs (Christensen et al., 2005). Thus, EwE may be seen as an important source of data enabling a better understanding of the variability of the trophic functioning between marine ecosystems. In fact, ecological indicators vary differently between ecosystems (Blanchard et al., 2010), and it appears necessary to better identify possible typical trophic behaviors. One possible approach to better understand and identify key indicators is inter-ecosystem type comparisons (Murawski et al., 2010). In fact, a comparative approach across ecosystem types could help identify common patterns and differences in ecosystems' trophic functioning and derived ecosystem indices (Legendre and Niquil, 2013).

The consideration of variability through the wide diversity of marine ecosystems has already been considered several decades ago. In fact, Ryther (1969) distinguished three types of ecosystem (provinces) with associated key parameters to estimate the global fish biomass in marine ecosystems: open oceans, coastal zones and upwelling areas. Although these hypotheses were based on few data and wrong guesses, it emphasized important possible variations in the

trophic functioning driven by abiotic and physical parameters. Several studies based on EwE models have shown since different trophic functioning according to various ecosystem types. Christensen and Pauly (1993a) revealed differences among ecosystem indices values, as the system productivity, biomass, primary production, partly related to different ecosystem types. They also showed that transfer efficiencies (TE) seemed to vary across ecosystems and trophic levels with a mean value of 9.2%. This last parameter is of particular interest: it has been defined by Lindeman (1942) (see Section 1.4), and is often assumed to vary around 10%, i.e. one-tenth of the production that enters a trophic level is transferred to the next one. Libralato et al. (2008) went further with a comparative study of this parameter over 91 Ecopath models: they distinguished temperate shelves and seas (14%), the tropical ones (10%), coastal areas and coral reefs (13%), upwellings (5%), and lagoons (11%). However, a global consensus has not yet been made regarding reliable values for TEs, that should be observed at the trophic level to better apprehend ecosystem functioning (Niquil et al., 2014), and seems to increase with fishing pressure (Coll et al., 2009; Heymans et al., 2012). Thus, further studies are needed to test the validity of these values and investigate in depth these trophic functioning principles.

Overall, only few meta-analyses based on a large collection of EwE models have been published to date, but they showed new insights into trophic functioning and its variability across ecosystems (e.g., Christensen, 1995; Christensen et al., 2014; Coll et al., 2013; Heymans et al., 2014, 2011). In this context, this chapter presents a meta-analysis based on 127 Ecopath models extracted from the EcoBase repository (see Appendix A). These models represent different marine ecosystems, and were used to analyze the variability of the trophic functioning between ecosystem types. First, EcoTroph was used to simulate all the models at an unexploited state and to compute the associated biomass, production, and kinetic trophic spectra. Trophic spectra

variability was analyzed considering two traits: the ecosystem type, and the latitude. First, a principal component analysis (PCA) was performed to apprehend biomass trophic spectra variability and explore the correlation structure between the different TL classes. Then, linear models were adjusted to statistically assess the differences among ecosystem types and compute mean trophic spectra by ecosystem type. Finally, several trophic indices were extracted from each ecosystem trophic spectrum and compared. A particular attention was put on the estimation of net transfer efficiencies from EcoTroph, and their variability across ecosystem types and TL ranges.

5.3 Materials and methods

5.3.1 Food web models and transposition into trophic spectra

This meta-analysis is based on 127 Ecopath models representing diverse marine ecosystems (see Figure 5.1 and Table F.1) extracted from EcoBase (see Appendix A). All the models were published (see references in Table F.1), used wet weight (in t.km^{-2}) as currency unit, and represented whole ecosystems. Each model was associated with a spatial shape enabling to locate it (see Chapter 2), and was classified within different ecosystem types (see Table F.1). Using expert knowledge, seven different ecosystem types were defined: reef, lagoon, bay, coastal, shelf-slope, upwelling, and ocean. The ecosystem types 'coastal, 'shelf-slope', and 'ocean' were defined according to the depth range covered by the model: the 'coastal' ecosystems corresponded to models representing the upper part of the continental shelf with a maximum depth lower or equal to 100 meters, the 'shelf-slope' ecosystems to models representing the continental shelf or the continental shelf and a part of the slope, and the 'ocean'

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ecosystems to models representing large oceanic areas. Additionally, the centroid of the spatial shape associated to each model was used to define the climatic zone of the model. Three climatic zones were defined based on latitude: tropical-subtropical (less than 30°N/30°S), temperate (in the range 30°N-58°N/30°S-58°S), and high latitude (greater than 58°N/58°S) (Pikitch et al., 2014).
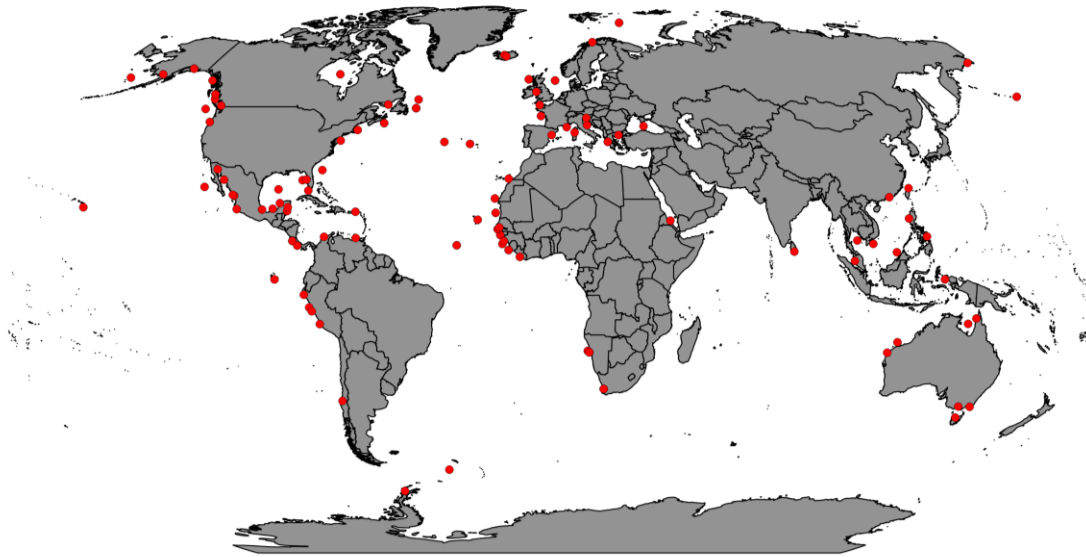
Figure 5.1 World map of the 127 EwE models used in this chapter, representing the centroids of the geographic extent of the models.

First, each Ecopath model was transposed into biomass (BTS), production (PTS), and kinetic trophic spectra (KTS) using the ET-Transpose routine. These representations correspond to the distribution of the biomass, the production, and the kinetic by trophic level class ($\Delta\tau=0.1$ TL; see Section 3.3). These trophic spectra did not account for detritus groups included in Ecopath (see Section 5.5.2). Then, using the ET-Diagnosis routine (see Section 3.3), trophic

spectra were simulated back to an unexploited state. This enabled a homogeneous comparison between the different ecosystems without accounting for differences in fishing pressure.

5.3.2 Trophic spectra analyses

As a first step, the variability of the 127 BTS was investigated using a principal component analysis (PCA). This method enables to describe and resume a complex dataset consisting in numerous covariates and supplementary variables. Thus, each trophic class comprised between TL=2 and TL=5.5 was used as a covariate in order to better apprehend BTS variability and explore the correlation structure between the different TL classes. The different ecosystem types were used as a supplementary variable to give a preliminary sense of their potential specific characteristics, as well as potential similarities. The impact of latitude classes was also explored for the different ecosystem types were such an analysis was possible (see Section 5.4.1), using the different latitude classes as a supplementary variable. Analyses were carried out using the FactoMineR R package (Lê et al., 2008).

In a second step, linear models (LMs) were used to investigate the variability of the 127 BTS, PTS, and KTS between the different TL classes and ecosystem types. The biomasses by trophic class were used as individuals, and TL classes and ecosystem types were as used as categorical variables (factors). The following LM was tested:

$$\log(B) = a + TL + EC + TL{:}EC \qquad (5.1)$$

where log(B) is the log-transformed biomass by trophic class, a is the intercept, and EC is the ecosystem type. Interaction effects were tested between the two categorical variables (corresponded to the ':' symbol in Eq. (5.1)). These interaction effects should reflect a different evolution of the biomass between each trophic class and ecosystem type. Identity-link functions

were used to relate the biomass to the categorical variables. Here, the link function was simply the mean response of the model, i.e., the mean biomass by TL class and ecosystem type. An analysis of variance was performed to verify the statistical significance of each factor and their interaction. Using the developed LM, a mean BTS was derived for each ecosystem type. Then, the differences observed between each ecosystem type were investigated for each trophic class using Pairwise t-tests. This test enables to investigate and statistically validate the differences between the different levels of a categorical variable.

These two steps were developed to demonstrate significant differences between the different TL classes and ecosystem types. Results (see Section 5.4.2) indicated the need to redefine the ecosystem type classification. Thus, in a third step, the latitude classes were integrated as an additional categorical variable to define new ecosystem types. The same methodology, i.e., the use of Eq. (5.1) and Pairwise t-tests, was applied to assess differences in the BTS between the redefined ecosystem types. Mean BTS by ecosystem type and associated confidence intervals were computed to compare their different characteristics. Finally, PTS and KTS were analyzed to explain differences observed between the different mean BTS. The same equation (Eq. (5.1)) was applied on the log-transformed production and kinetic to produce mean PTS and KTS by ecosystem type. Pairwise t-tests were performed to statistically assess associated differences by TL classes and ecosystem types.

5.3.3   Calculation of trophic indices

Different trophic indices derived from the BTS were calculated for each ecosystem:

- The total biomass (B_{tot}) was calculated as the sum of the biomass for TL classes comprised between TL=2 and TL=5.5 (excluding primary producers)

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- The predator biomass (B_{pred}) was calculated as the sum of the biomass for TL classes comprised between TL=3.3 and TL=5.5.

- The high trophic level index (HTI; Bourdaud, 2014) corresponded to the proportion of biomass at TL≥4 compared to the total biomass

- The mean TL of the biomass (TL_{mean}) was calculated as (Eq. (5.2)):

$$TL_{mean} = \frac{\sum_{\tau=2}^{5.5} B_{\tau} \times \tau}{\sum_{\tau=2}^{5.5} B_{\tau}} \tag{5.2}$$

- The mean TL of the predator biomass (TL_{pred}) was calculated as in Eq. (5.2), but accounting for biomasses comprised between TL=3.3 and TL=5

Differences in the trophic indices between ecosystem types were analyzed using Pairwise t-tests.

Additional trophic indices were calculated using the different PTS. Mean net transfer efficiencies (NTEs) were estimated across different TL ranges: between TL=1 and TL=2, TL=2 and TL=2.9, TL=3 and TL=3.9, TL=4 and TL=5.5. More precisely, additional LMs were adjusted as (Eq. (5.3)):

$$\log(P) = a + TL + EC + TL{:}EC \tag{5.3}$$

where log(P) is the log-transformed production by trophic class. The TL classes were treated as a continuous variable, so that the NTE was equal to the exponential of the slope of the adjusted linear regression. In fact, NTE is defined as (Eq. (5.4); see Section 3.3):

$$NTE = exp(-\mu) = exp\left(log\left(\frac{\Phi_{\tau+\Delta\tau}}{\Phi_{\tau}}\right) \times \frac{1}{\Delta\tau}\right) = exp\left(\frac{log(\Phi_{\tau+\Delta\tau}) - log(\Phi_{\tau})}{\tau + \Delta\tau - \tau}\right) \tag{5.4}$$

This last element included in the exponential corresponded to the slope of a linear regression adjusted on the log-transformed flow of biomass (equivalent to the production when used as a ratio) between defined TL classes. Thus, we implemented such linear regressions (Eq. (5.3))

between defined TL ranges, and tested the significance of each term comprised in the LMs using analyses of variance. Thus, NTEs differed between ecosystem types if the interaction term was statistically significant.

5.4   Results

5.4.1   Global overview on the modeled ecosystems

The 127 Ecopath models represented different ecosystem types and latitude classes (Table 5.1). Overall, the shelf-slope type represented around 60% (75 models) of the total model number, and the other types between 4 and 9% of the models. The latitude classes were dominated by the tropical class ('0-30') comprising 65 models (around 50% of the models), and the temperate one ('30-58') comprising 51 models (40% of the models). Logically, the 'reef' and 'lagoon' type were all located in tropical latitudes, and 'upwelling' models were all located in tropical and temperate latitudes. However, this distribution by ecosystem type and latitude class also showed that few 'bay' models were located in temperate and high latitudes. This was also the case for the 'ocean' and 'coastal' types, the last one having no records for high latitudes. These considerations directly impacted the analysis, and the associated consideration of latitude effect within each ecosystem type.

Table 5.1 Distribution of the 127 Ecopath models by ecosystem type and latitude class.

		Latitude class			Total
		0-30	*30-58*	*58-90*	
Ecosystem type	*bay*	9	1	2	12
	coastal	6	2	0	8
	lagoon	5	0	0	5
	ocean	2	2	1	5
	reef	10	0	0	10
	shelf-slope	26	41	8	75
	upwelling	7	5	0	12
Total		65	51	11	127

5.4.2   Identification of typical trophic spectra

Results of the PCA performed on the 127 BTS showed that TL classes explained a high percentage of the total variance (around 73%; Figure 5.2). This was quite logical considering the important variations of the biomass across TL classes. The first PCA axis was highly correlated to high TL classes comprised between 4 and 4.5, whereas the second one corresponded to intermediate TL classes comprised between 2.7 and 3.1 (see Figure 5.2a, and Table F.2). The individuals factor map (Figure 5.2b) showed differences between the different ecosystem types: the 'shelf-slope' ecosystems were mostly located in the center of the map, the 'bay' and 'lagoon' ecosystems seemed to be mostly displayed on the left part, whereas the 'reef' and 'upwelling' ecosystems were displayed on the right top part. All this information was summarized using the barycenter of each ecosystem type and the associated confidence ellipses calculated by the PCA analysis (Figure 5.2c).

Figure 5.2 Results of the PCA showing (a) the projection of the different TL classes on the two dimensions included in the analysis, (b) the projection of the 127 ecosystems colored by ecosystem type, (c) the location of the barycenter and confidence ellipses associated to each ecosystem type, and (d) the location of the barycenter and confidence ellipses associated to each latitude class for a subset comprising the 'ocean', 'shelf-slope' and 'coastal' ecosystems only.

The 'upwelling' ecosystems seemed to differ from the other types; the position of the barycenter and the associated confidence ellipse indicated a high biomass for high and intermediate trophic levels. The 'reef' ecosystems were also different from the other types with a relative position indicating a high biomass of intermediate trophic levels. The form of the ellipse indicated a high variability regarding the biomass of high trophic levels. On the contrary, 'lagoon' ecosystems seemed to be characterized by a low biomass at high trophic levels and a high one at intermediate trophic levels. The 'bay' ecosystems had an extended confidence ellipse overlapping the 'lagoon' and 'coastal' ecosystems indicating a possible high variability in biomass with characteristics varying between ecosystems. Thus, some 'bay' ecosystems had similar characteristics with 'lagoon' ones, and others 'coastal' properties. Finally, the 'shelf-slope' and 'ocean ecosystems were close to each other: the 'shelf-slope' relative position seemed to indicate a higher biomass at high trophic levels compared to the 'ocean'. The 'coastal' ecosystems were highly variable with an ellipse overlapping the 'shelf-slope' and 'ocean' ones. The size of the ellipse was also function of the number of models included in each ecosystem type indicating the need for further analysis to properly analyze each ecosystem type.

Since the 'coastal', 'shelf-slope', and 'ocean' ecosystems were quite similar compared to the other ecosystem types, a second PCA was developed on the corresponding ecosystems only (88 ecosystems, see Table 5.1), using the TL classes (between TL=2 and 5.5) as covariates, and the latitude class as a supplementary variable. The two PCA axes were correlated to the same trophic classes compared to the previous run, and explained around 70% of the total variance. Results indicated different properties associated to each latitude class (Figure 5.2d): tropical ecosystems ('0-30') seemed to be defined by lower biomass at high trophic levels compared to the temperate and high latitudes ones (respectively '30-58' and '58-90').

Then, we developed LMs to further investigate differences between ecosystem types (Eq. (5.1)). Results indicated that each term of Eq. (5.1) was statistically significant (TL, EC, and TL:EC with a p-value<0.05). Furthermore, based on variance analyses and Akaike information criterion, the model including the TL, the ecosystem type, and their interaction was statistically better than a model including the TL effect only, or a model including TL and ecosystem type effects. The LM enabled to derive mean BTS by ecosystem type and associated confidence intervals (Figure 5.3).
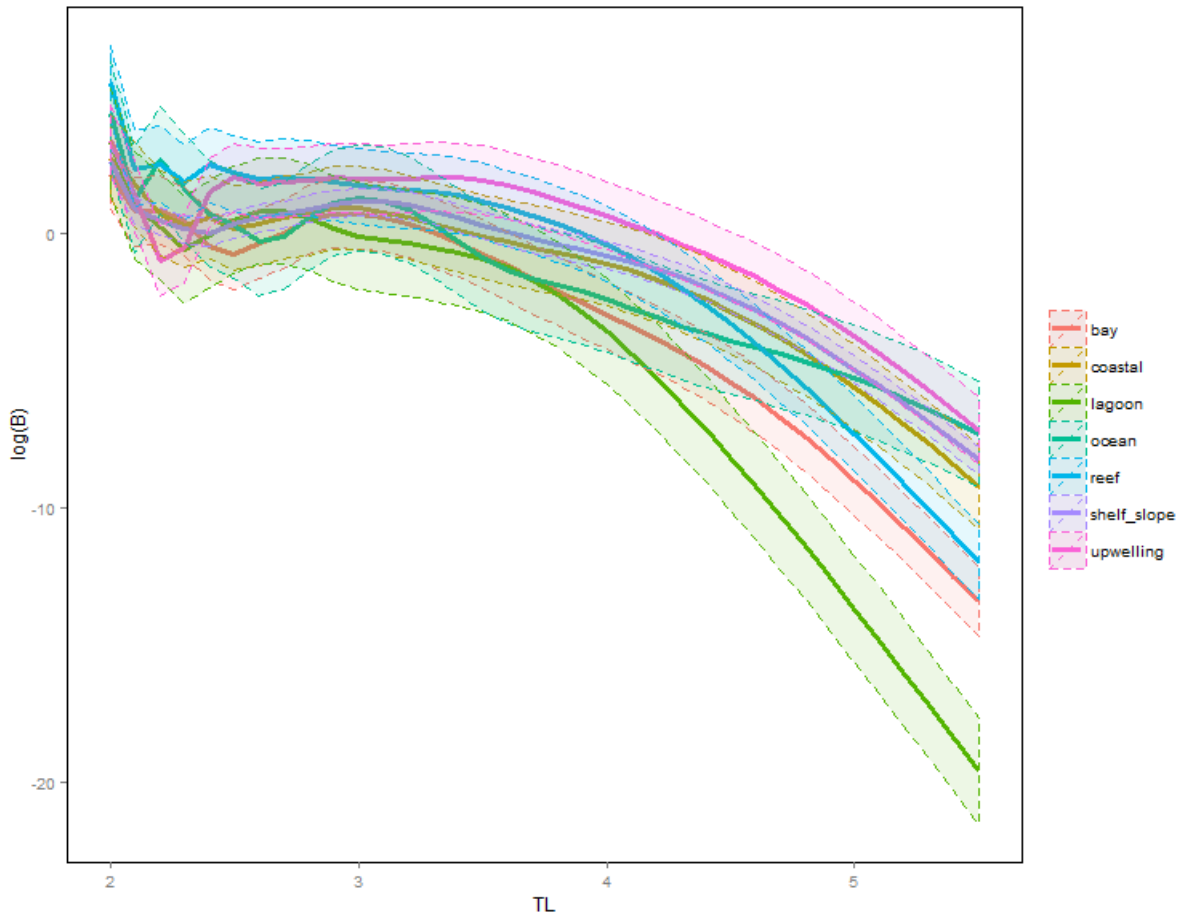
Figure 5.3 Mean BTS by ecosystem type derived from the LM.

These mean BTS showed different trends between ecosystem types. The 'reef' and 'lagoon' ecosystems were characterized by higher biomass at low trophic levels (TL classes comprised between 2 and 2.4) compared to the other ecosystem types. For intermediate trophic levels (comprised between TL=2.5 and TL=3.2), the 'reef' and 'upwelling' exhibited higher biomass. 'Lagoon' ecosystems were characterized by lower biomass for high TLs, with a BTS having a strong slope for TLs≥4. On the contrary, the 'upwelling', 'shelf-slope' and 'coastal' ecosystems seemed to be characterized by high biomass for high trophic levels. The 'bay' and 'reef' ecosystems exhibited intermediate positions with lower biomass compared to the previously mentioned ecosystem types, and higher compared to the 'lagoon' ecosystems. Overall, 'shelf-slope' and 'coastal' ecosystems were very similar, and, in a lesser extent, similar to 'ocean' ecosystems which had a large confidence interval (partly explained by the low number of associated ecosystems). In order to validate observed differences and similarities, Pairwise t-tests were performed for each trophic class (between TL=2 and TL=5.5) on the mean value of the log-transformed biomass in relation to the ecosystem type. A pooled standard deviation was used to perform all the tests, since it was more precautious considering the low number of models associated to several ecosystem types (see Table 5.1). Results indicated that there were no statistical differences between the 'ocean', 'shelf-slope', and 'coastal' ecosystems. There were also no differences between the 'reef' and 'coastal' ecosystems (Table 5.2). On the contrary, 'lagoon' ecosystems were different from other ecosystem types for a high number of TL classes. This was also the case for the 'bay' and 'upwelling' ecosystems. Thus, Pairwise t-tests validated observations made on the mean BTS, and indicated the need to pool together the 'coastal', 'ocean' and 'shelf-slope' ecosystems into a new ecosystem type.

Table 5.2 Results of the Pairwise t-tests cross-comparing each ecosystem type mean log-transformed biomass to all other types. Numbers given correspond to the total number of trophic class where a statistical difference is observed (p-value<0.1; number in brackets where p-value<0.05).

	bay	coastal	lagoon	ocean	reef	shelf-slope
coastal	10 (6)					
lagoon	11 (8)	16 (16)				
ocean	3 (0)	0 (0)	13 (12)			
reef	15 (15)	0 (0)	24 (24)	6 (5)		
shelf-slope	21 (20)	0 (0)	18 (18)	0 (0)	4 (0)	
upwelling	27 (27)	8 (7)	26 (25)	12 (11)	10 (0)	10 (9)

Thus, 'coastal', 'ocean', and 'shelf-slope' ecosystem types were pooled together into the 'shelf-slope' type, and additional LM and Pairwise t-tests were conducted by replacing the ecosystem type by the different latitude classes as a factor in Eq. (5.1). Results indicated that each term of the LM was statistically significant (p-value<0.05). Furthermore, based on variance analyses and Akaike information criterion, the model including the TL, the latitude class, and their interaction was statistically better than a model including the TL effect only, or a model including TL and latitude class effects. The LM enabled to derive mean 'shelf-slope' BTS by latitude class and their associated confidence intervals (Figure 5.4). This analysis showed that temperate and high latitude 'shelf-slope' ecosystems were characterized by higher biomass for intermediate and high trophic levels, but lower biomass for low TLs. In order to statistically assess observed differences, we performed Pairwise t-tests. Results indicated that tropical 'shelf-slope' were statistically different from the two other latitude classes, but that there were no differences between the temperate and high latitudes classes. Thus, we ended up with a new ecosystem classification differentiating between: 'bay', 'lagoon', 'reef', 'upwelling', 'shelf-trop'

(corresponding to the tropical latitude class), and 'shelf-temp' (corresponding to the temperate and high latitudes classes).
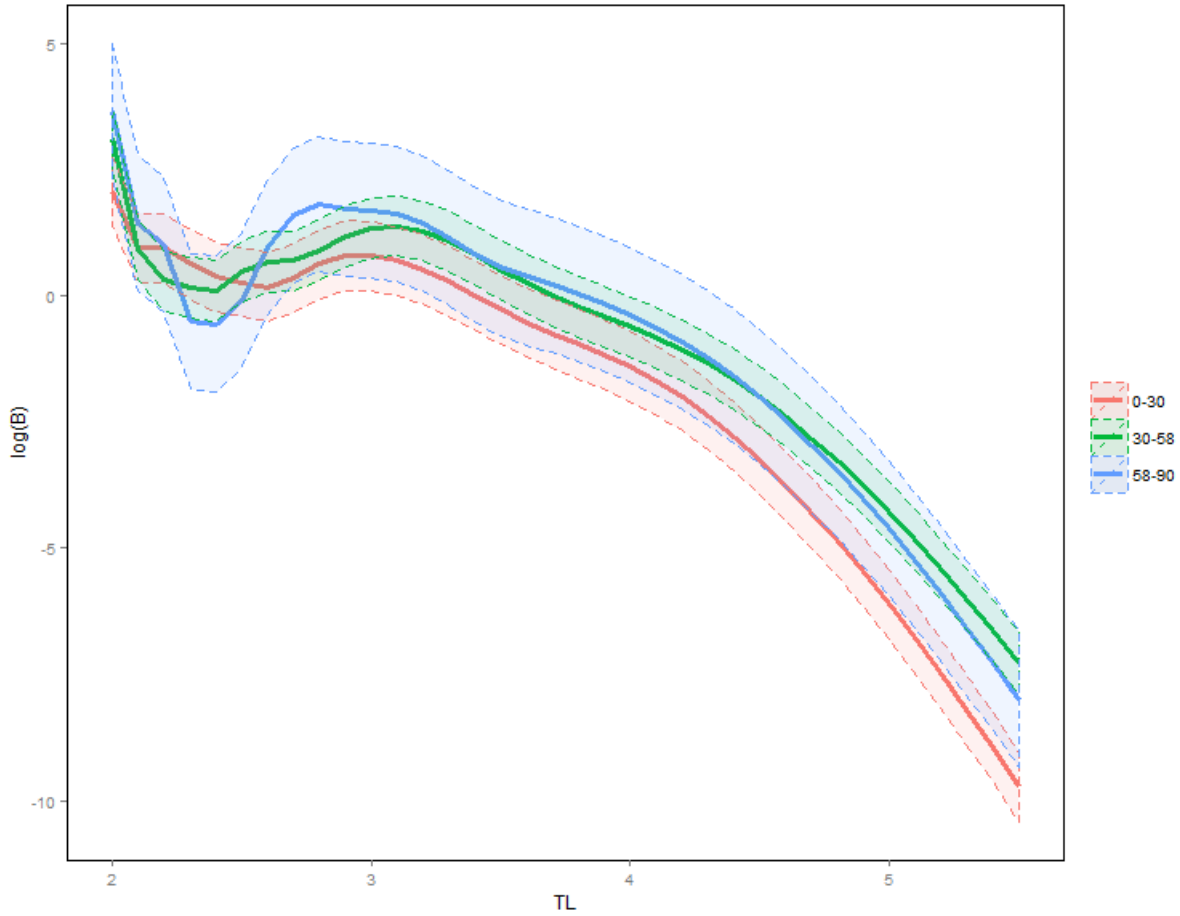
Figure 5.4 Mean BTS by latitude class derived from the LM for the newly defined 'shelf-slope' ecosystem type.

Finally, we implemented LM (Eq. (5.1)) and Pairwise t-tests to test the new ecosystem classification and compute associated mean BTS. Results indicated that each term integrated in the LM was statistically significant (p-value<0.05). Furthermore, the model including the TL, the ecosystem type, and their interaction was statistically better than a model including the TL effect

only, or a model including TL and ecosystem type effects. The LM enabled to derive mean BTS by ecosystem type and associated confidence intervals (Figure 5.5).
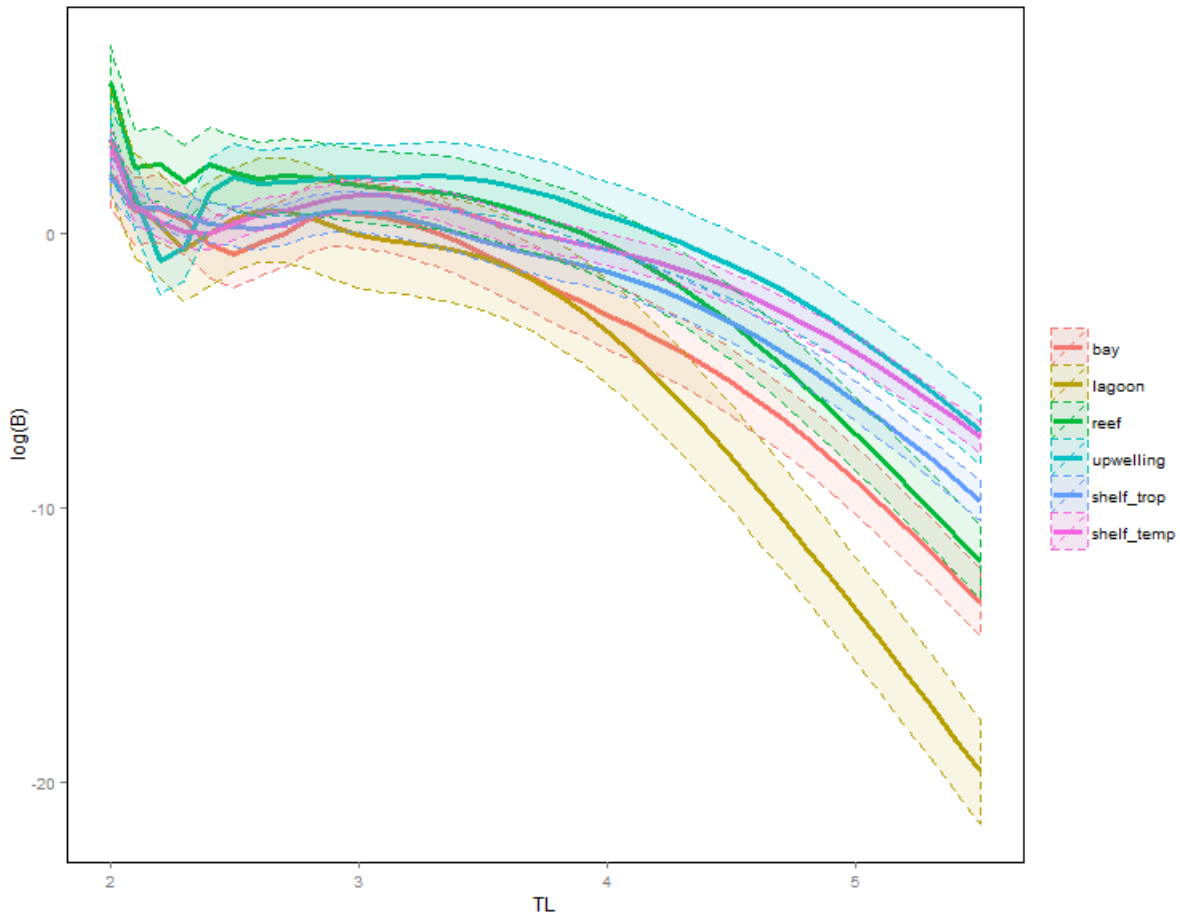
Figure 5.5 Mean BTS by lastly defined ecosystem type derived from the LM.

Results differed compared to the first developed ecosystem classification since two new ecosystem types were included ('shelf-temp' and 'shelf-trop'). They showed that 'shelf-temp' ecosystems were characterized by higher biomass for high TLs compared to the 'shelf-trop' ecosystems. In order to validate observed differences and similarities, Pairwise t-tests were

performed for each trophic class (between TL=2 and TL=5.5) on the mean value of the log-transformed biomass in relation to the ecosystem type. As previously mentioned, a pooled standard deviation was used to perform all the tests. Results indicated that all ecosystem types were statistically different from each other on different TL ranges (see Table 5.3, and details in Table F.3). Differences were mostly recorded for high trophic levels (TL≥3.3), but also for intermediate trophic levels ('reef' and 'upwelling' ecosystems differed from the other ecosystem types).

Table 5.3 Results of the Pairwise t-tests cross-comparing each ecosystem type mean log-transformed biomass to all other types. Numbers given correspond to the total number of trophic class where a statistical difference is observed (p-value<0.1; number in brackets where p-value<0.05).

	bay	lagoon	reef	upwelling	shelf-trop
lagoon	11 (10)				
reef	17 (15)	25 (24)			
upwelling	29 (27)	27 (26)	11 (9)		
shelf-trop	18 (17)	17 (16)	10 (9)	24 (21)	
shelf-temp	23 (23)	24 (24)	10 (7)	8 (8)	25 (19)

The last step of this analysis was to explain the differences observed between the different mean BTS using the associated mean PTS and KTS. The same methodology based on LMs and Pairwise t-tests was used. As in previous analyses, results indicated that each term integrated in the LM was statistically significant (p-value<0.05) for both the log-transformed production and kinetic. Furthermore, models including the TL, the ecosystem type, and their interaction were statistically better than models including the TL effect only, or models including TL and ecosystem type effects. The LMs enabled to derive mean PTS and KTS by ecosystem type and associated confidence intervals (Figure 5.6).

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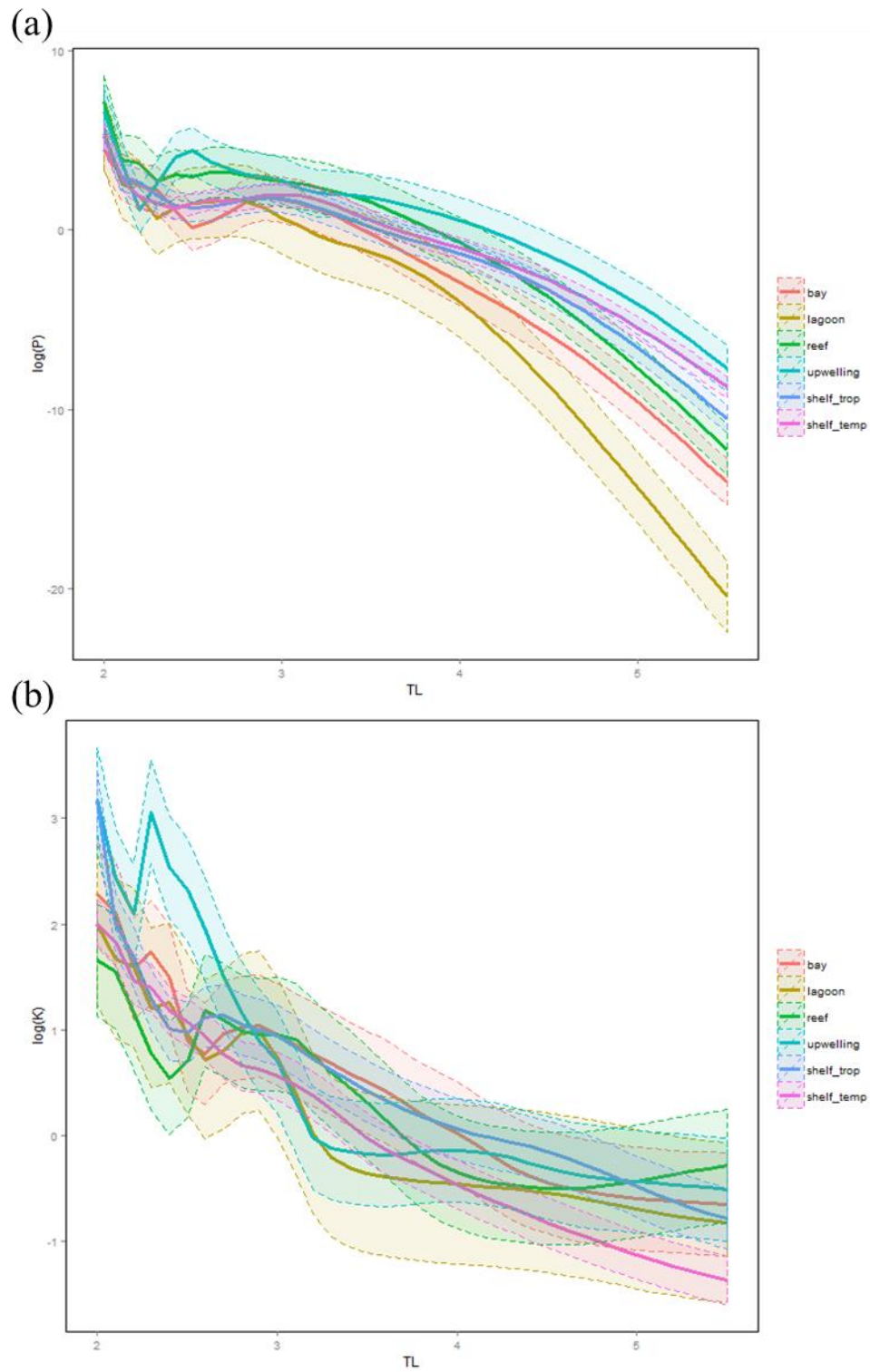
Figure 5.6 Mean (a) PTS and (b) KTS by ecosystem type, derived from LMs.

The mean PTS by ecosystem type showed relative similar trends compared to the mean BTS (Figure 5.5, and Figure 5.6). However, some differences were noticeable, notably for the 'upwelling' PTS which seemed to have a higher production for TLs around 2.5 compared to the other ecosystem types. The mean KTS exhibited differences by ecosystem type. Overall, the kinetic decreased along the trophic level. However, the 'upwelling' ecosystems seemed to be characterized by a specific kinetic with a peak for TLs around 2.3, and then a fast decrease with a mean KTS joining other ecosystem types' KTS. On the contrary, 'reef' ecosystems seemed to have lower kinetic values for TLs around 2.3 compared to the other types. A general trend for mean KTS was a decrease until TLs around 2.5, then an increase for TLs between 2.5 and 3, and finally a slow decrease for higher TLs. This was not the case for the 'shelf-trop' ecosystems that also exhibited a specific mean KTS compared to the other types, and notably the 'shelf-temp' ecosystems. In fact, 'shelf-trop' KTS seemed to continuously decrease along the trophic level, and had lower values for high TLs compared to the other types. These differences in mean PTS and KTS were assessed using Pairwise t-tests (Table 5.4 and Table 5.5, see details in Table F.4 and Table F.5).

Table 5.4 Results of the Pairwise t-tests cross-comparing each ecosystem type mean log-transformed production to all other types. Numbers given correspond to the total number of trophic class where a statistical difference is observed (p-value<0.1; number in brackets where p-value<0.05).

	bay	lagoon	reef	upwelling	shelf-trop
lagoon	10 (9)				
reef	14 (11)	25 (25)			
upwelling	25 (25)	25 (25)	11 (7)		
shelf-trop	16 (14)	20 (17)	6 (3)	20 (14)	
shelf-temp	19 (18)	24 (24)	2 (0)	13 (11)	0 (0)

Table 5.5 Results of the Pairwise t-tests cross-comparing each ecosystem type mean log-transformed kinetic to all other types. Numbers given correspond to the total number of trophic class where a statistical difference is observed (p-value<0.1; number in brackets where p-value<0.05).

	bay	**lagoon**	**reef**	**upwelling**	**shelf-trop**
lagoon	0 (0)				
reef	0 (0)	0 (0)			
upwelling	2 (1)	1 (0)	4 (4)		
shelf-trop	0 (0)	0 (0)	1 (1)	6 (3)	
shelf-temp	0 (0)	0 (0)	5 (4)	11 (9)	22 (21)

Results showed that differences observed between mean BTS were mainly driven by differences in production. In fact, results of the Pairwise t-tests were relatively similar between BTS and PTS (Table 5.3 and Table 5.4). However, significant differences in kinetic were observed for three ecosystem types. The 'upwelling' ecosystems had different KTS for TLs around 2.5 compared to the other ecosystem types (Table 5.5 and Table F.5). 'reef' ecosystems also had distinct kinetic for low TLs compared to the 'upwelling' and 'shelf-trop' ecosystems, and for high TLs compared to the 'shelf-temp' type. Finally, differences observed between the 'shelf-temp' and 'shelf-trop' types were driven by kinetic, since their mean PTS were statistically similar but not their mean KTS.

5.4.3   Trophic indices analysis

First, trophic indices extracted from the BTS were analyzed. The total biomass (B_{tot}; Figure 5.7a) was significantly higher for 'reef' ecosystems compared to the other types. This index exhibited very strong values due to high biomass of invertebrates (e.g., echinoderms, mollusks, worms) in the corresponding Ecopath models. Looking at the predator biomass (B_{pred}; Figure 5.7b), the 'reef' and 'upwelling' ecosystems were characterized by significantly higher

values compared to the other types. This was logical considering observations made on the mean BTS emphasizing greater biomass for intermediate TLs for these two types, and greater biomass for high trophic levels for the 'upwelling' ecosystems (see Section 5.4.2). This last observation was validated by the HTI showing significantly greater values for the 'upwelling' ecosystems compared to the other types (around 4%; Figure 5.7c). The 'shelf-trop' and 'shelf-temp' ecosystems seemed also to have higher HTI (around 2%) compared to the 'lagoon', 'reef', and 'bay' ecosystems. However, differences were not statistically significant. Concomitantly, the mean TL (TL_{mean}; Figure 5.7d) was significantly higher for 'upwelling' that exhibited a median value around 2.8. As observed on the HTI, the 'shelf-temp' and 'shelf-trop' ecosystems held an intermediate position with a median value slightly superior to 2.4. Finally, the mean TL of the predator biomass (TL_{pred}; Figure 5.7e) showed no significant differences between ecosystem types, except between 'shelf-temp' and 'lagoon' ecosystems (due partly to the number of models by ecosystem type). However, observed trends indicated a higher TL_{pred} for the 'shelf-temp', 'shelf-trop' and 'upwelling' ecosystems compared to the three other types. This was also logical considering observations made on the mean BTS by ecosystem type.

Then, mean net transfer efficiencies were calculated for different TL ranges (Table 5.6). Results showed that the ecosystem type-TL interaction had a statistically significant impact only for NTEs calculated over TL=3 to 3.9, TL=4 to 4.9, and TL=2 to 5.5. Overall, NTEs seemed to increase until TL=2.9, and then to decrease until TL=5.5. This was not the case for the 'upwelling' ecosystems that exhibited a high NTE over the TL range 3-3.9 compared to the other types and other NTE estimates. However, by forcing the ecosystem type-TL interaction (not significant, partly due to the low number of models in some ecosystem types), we obtained a high NTE for 'upwelling' ecosystems over the TL range 2-2.9 (25.18%). Thus, 'upwelling'

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ecosystems appeared to be characterized by high NTEs for TLs ranging from 2 to 3.9. Only the 'shelf-temp' ecosystems had a higher NTE for the TL ranges 4-5.5, and 2-5.5. On the contrary, the 'lagoon' and 'bay' types were characterized by low transfer efficiencies explaining the low biomasses previously observed. However, they seemed to be characterized by higher NTEs compared to the other types from TL=1 to TL=2 (around 12%, ecosystem type-TL interaction not significant). Overall, from TL=2 to 5.5, 'upwelling' and 'shelf-temp' ecosystems exhibited higher NTEs (around 4.4%) compared to the other types. 'shelf-trop' held an intermediate position with a NTE of 2.7%.

Table 5.6 Net transfer efficiencies (NTEs, in %) estimated for different TL ranges using LMs adjusted on the log-transformed production coming from the PTS ('*' indicates a significant effect of the associated factor or interaction in the LM).

	NTE 1-2		NTE 2-2.9		NTE 3-3.9		NTE 4-5.5		NTE 2-5.5	
bay	2.82		5.65		0.91 *		0.06 *		0.92 *	
lagoon	12.17		7.07		1.70 *		0.002 *		0.15 *	
reef	12.40	5.71 *	5.91	8.33 *	3.56 *	3.67 *	0.04 *	0.22 *	1.02 *	2.60 *
upwelling	7.57		25.18		16.17 *		0.42 *		4.36 *	
shelf-trop	4.76		5.57		3.93 *		0.20 *		2.74 *	
shelf-temp	5.69		9.89		3.73 *		0.56 *		4.38 *	
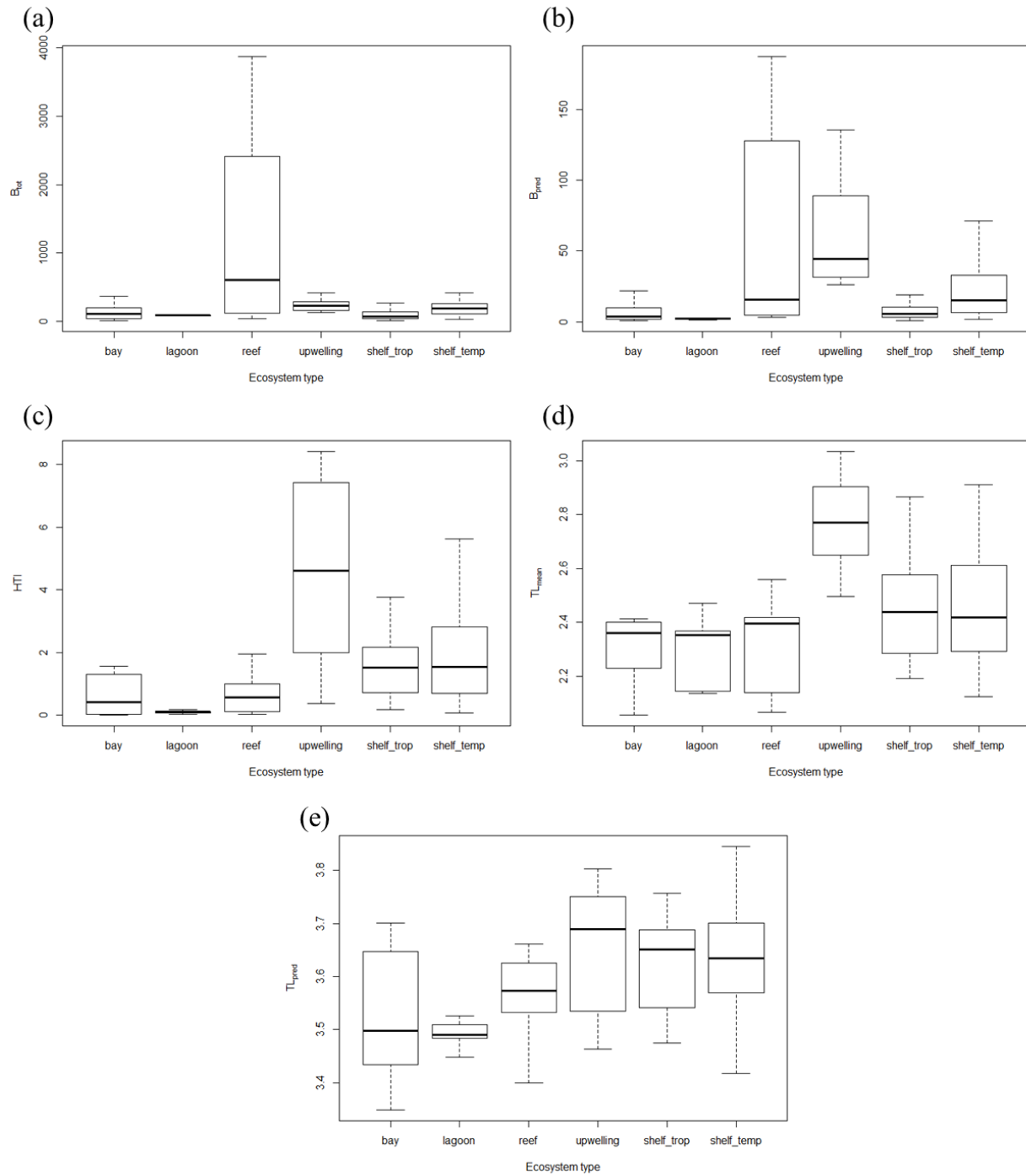
Figure 5.7 Boxplots of the trophic indices by ecosystem type: (a) the total biomass, (b) the predator biomass, (c) the high trophic level index, (d) the mean TL of the biomass, and (e) the mean TL of the predator biomass.

5.5   Discussion

5.5.1   Typical trophic functioning of marine ecosystems

Results showed that new insights into marine ecosystems' trophic functioning can be provided using a large database of Ecopath models. Furthermore, the use of EcoTroph enables a homogeneous comparison between ecosystem models using trophic spectra. This meta-analysis is the first study using such a tool to analyze a large number of marine ecosystems, and to identify typical trophic functioning. In fact, results showed that ecosystem types, such as the ones defined for the purpose of this analysis, are characterized by different trophic functioning, i.e., different mean trophic spectra and associated trophic indices.

Overall, the 'lagoon' and 'bay' ecosystems seemed to be defined by a low biomass for high trophic levels. This was associated with a lower production and smaller transfer efficiencies for TLs≥3. On the contrary, 'upwelling' ecosystems were characterized by a high biomass at high TLs, and a high mean trophic level compared to the other types. Moreover, their net transfer efficiencies had high values for TLs≥3. These differences emphasized opposed trophic functioning between 'upwelling', and 'bay' and 'lagoon' ecosystems. In fact, high transfer efficiencies are usually related to system with fewer pathways between trophic levels in the food web, while ecosystems such as lagoons and bays are often characterized by a high diversity at low trophic levels and, thus, reduced mean transfer efficiency (Baird et al., 1991; Heymans et al., 2014; Jarre-Teichmann et al., 1998; Vasconcellos et al., 1997). However, such a high NTE compared to other ecosystem types was not previously calculated by study based on large number of Ecopath models (Libralato et al., 2008). This difference was explained by models included in each dataset: Libralato et al. (2008) considered three models of upwelling

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ecosystems, of which two were not included in this analysis due to doubts on the corresponding collected Ecopath models included in EcoBase (Peru upwelling; Jarre-Teichmann and Pauly, 1993). Furthermore, 'upwelling' ecosystems seem to have a specific flow kinetic with high values for low TLs (a peak in KTS was observed around TL=2.3).

'Reef' ecosystems were characterized by a high biomass for low and intermediate TLs, and thus a high total biomass. This was consistent with previous meta-analysis performed on a large collection of Ecopath models (Heymans et al., 2014). Their kinetic was also typical for low TLs (around TL=2.5) with smaller values compared to the other types. Finally, 'shelf-slope' ecosystems were defined by a high biomass for high TLs compared to the 'reef', 'lagoon', and 'bay' types, and thus a relatively higher HTI and mean TL of the predator biomass. They also had higher NTEs for TLs≥3 compared to these three types, but had a smaller production compared to the 'upwelling' ecosystems. Differences between the 'shelf-temp' and 'shelf-trop' ecosystems were mostly driven by differences in the kinetic. This showed a possible impact of the latitude, and thus the temperature, on the kinetic. This impact has already been shown, and the kinetic seems to increase with higher sea surface temperature (Gascuel et al., 2008).

All these elements were summarized using the biomass, production, and kinetic trophic spectra. These graphic representations showed a high potential to be used to study and characterize marine ecosystems (Gascuel et al., 2011, 2005). Furthermore, indices derived from food web models as Ecopath or EcoTroph (through the use of trophic spectra) has been shown to be useful indicators to assess the good environmental status included in the Marine Strategy Framework Directive of the European Union (Lassen et al., 2013; Rombouts et al., 2013). Several studies showed the need to investigate more deeply changes in food web indices considering different ecosystem traits and fishing impacts (Heymans et al., 2014, 2012). This

analysis emphasized the need to account for the ecosystem type in order to define reliable ecosystem indices and their associated reference levels and thresholds that are needed for ecosystem-based management advice (Samhouri et al., 2010; Shin et al., 2010).

5.5.2 Using Ecopath and EcoTroph to analyze the trophic functioning

This analysis showed interesting trends regarding the trophic functioning of marine ecosystems. However, it is based on a large number of Ecopath models with inherent problems due to the modeling technique. In fact, the quality of the models was not accounted for in the different analyses. First, there was no uncertainty testing in model inputs (Essington, 2007; Plagányi and Butterworth, 2004). The origin of the data was not precisely known and accounted for in this analysis, as well as the proportion of groups' biomass and P/B ratios used as inputs or estimated by the model. The Pedigree index has been developed to score each model based on which data are used as input, as well as their origin (Morissette, 2007). However, this score was calculated for only 17% of the models (recorded for 22 models in EcoBase), and it was thus not possible to use it. Potential interesting indicators to be included in this analysis could be the proportion of the groups having the biomass as an input, and the P/B ratio as an input. In fact, these two parameters are directly used in EcoTroph to compute the associated biomass and production trophic spectra.

Furthermore, the structure of the model was not accounted for. An indicator of the structure could be the number of groups included in each model. In fact, Ecopath models used in this analysis range from early models created in the 1990s with fewer trophic groups to newer models. Well, it has been shown in Chapter 2 that the complexity of the models increased with the publication year. Thus, early models could be less complex and well defined compared to

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more recent models. However, no general rule can be drawn from these observations, since the quality of the model depends also on the quality of input data, and some recent models also include a small number of groups (see Chapter 2). It has been shown that the structure of Ecopath models can have an impact on the computed ecological indicators (Fulton et al., 2005; Heymans et al., 2014). Thus, it could be interesting to integrate it in trophic functioning meta-analysis. However, the number of group is not the only indicator of the structure of the model. In fact, it does not reflect the construction details for all the biological compartments, notably for low trophic levels. EcoBase integrates a taxonomic/trophic guild classification of the Ecopath groups distinguishing between detritus, primary producers (two categories: phytoplankton and other primary producers), benthos groups, zooplankton, bacteria, mollusks (two categories: cephalopods and other mollusks), crustaceans, fishes, mammals, birds, and reptiles (e.g., turtles). It could be interesting to integrate a ratio of the number of invertebrate groups compared to the total number of groups to better apprehend the structure of associated Ecopath models, and to integrate it in future meta-analyses.

These elements also reflect the need to better apprehend the role of primary producers and detritus groups in Ecopath and EcoTroph. Detritus groups were not included in the EcoTroph analysis developed in this study. In fact, the corresponding biomass is usually not precisely calculated in corresponding Ecopath models since it is possible to set by default the value to 1. Thus, the representation of detritus groups and the potential associated microbial loop are usually not well defined in Ecopath models. Furthermore, the impact of detritus group on the production in ecosystem is not properly accounted for in EcoTroph equations. In fact, since no P/B ratio is defined in Ecopath, the calculation of primary production is misrepresented by

EcoTroph. As a result, further work is needed to better integrate the detrital production in EcoTroph, as well as precise estimate of the associated biomass in Ecopath.

Then, this study is based on 127 Ecopath models that were classified into different ecosystem types. Some types contained a few models only, as the 'bay' and 'ocean' ecosystems. Such ecosystem types were not well analyzed, and need to be studied in depth. In fact, the high variability within 'bay' ecosystems could be related to the latitude, and the 'ocean' ecosystems could have a different trophic functioning compared to the continental shelves or coastal ecosystems. Thus, it appears important to gather a larger number of Ecopath models to perform a powerful meta-analysis, and disentangle potential additional differences in the defined ecosystem types. The impact of fishing was also not accounted for in this analysis. However, it has been shown that ecological and trophic indices vary according to fishing pressure, and can be useful to detect fishing impacts on the trophic functioning (Heymans et al., 2014; Shannon et al., 2014). It could be interesting to simulate different fishing scenarios on the mean trophic spectra estimated by ecosystem type. This could enable to analyze and assess the comparative resistance of the different types to different fishing impacts.

Finally, the mean KTS by ecosystem type were directly derived from the production and biomass trophic spectra. However, it can be estimated using different data, notably the natural mortality of each Ecopath groups. Gascuel et al. (2008) used this method to develop a model for the kinetic as a function of the trophic level and the temperature. This relation needs to be further investigated by analyzing a larger dataset, and by taking into account the potential effect of ecosystem types. In fact, the mean KTS by ecosystem type showed a distinct kinetic for 'upwelling' ecosystems, and in a lesser extent for 'reef' ecosystems. Ecosystem types also

exhibited different net transfer efficiencies. This was logical considering differences in production and associated trophic functioning. NTE estimates appear low compared to usual Ecopath TE values (see Libralato et al., 2008), notably for the NTE estimated between TL=1 and 2. This estimate does not correspond to the total transfer efficiency between primary producers and secondary producers, as it is a ratio between the trophic level class 1 and 2. In fact, a part of production primary production is also directly transferred to the trophic class 2.1, 2.2… It corresponds to a value used in EcoTroph to initialize the secondary production. Overall, other NTE estimates appear also low compared to Ecopath value. This is logical considering the fact that the calculation methodology is not the same: EcoTroph calculates a ratio of log-transformed production, whereas Ecopath calculation is based on precise processes (respiration, excretion, non-predation mortality) and a geometric mean between TL II and IV. Thus, further analyses are needed to better link NTE coming from EcoTroph, and TE coming from Ecopath.

In conclusion, results provide new insights into marine ecosystems' trophic functioning. The identification of typical trophic functioning is of particular interest, since trophic indices are needed to better apprehend ecosystem functioning variability, and to furnish basis for an ecosystem approach to fisheries. Further analyses could precise results obtained in this analysis by incorporating more Ecopath models, taking into account the structure and quality of the models, and accounting for potential fishing impacts.

Chapter 6: General conclusions and perspectives

6.1 Gathering EwE models

This thesis represents one of the first attempts to provide all scientists with a general database of EwE models. In fact, an important aspect of presented analyses was the supporting data gathered into EcoBase (see Appendix A). EcoBase was designed to gather all data coming from Ecopath model, and to answer precise needs expressed by scientists. Thus, informative metadata were also collected to provide a comprehensive identification of associated ecosystems, model structure and history. However, the future of EcoBase is still uncertain. Thus, it appears important for the EcoBase project to be fully incorporated within the Ecopath Research and Development Consortium. It would enable other scientists to manipulate, improve and use this information repository to make it a powerful tool serving fisheries research interests. 435 unique Ecopath models were recorded in EcoBase, of which 303 models were associated with a collected Ecopath model (a EwE database Access file) and 132 with a publication only. These 303 unique models associated with a EwE database file corresponded in reality to 431 models as duplicates were obtained when merging the different existing EwE model collections from Lyne Morissette, Francisco Arreguín-Sánchez, and Villy Christensen (see Appendix A). Each model was compared to the supporting references to choose which ones to select when performing meta-analyses. In fact, models were in a lot of cases different compared to the associated references for different reasons: not balanced, different versions compared to paper (improved or previous versions), imprecise reconstruction... We selected 127 models for our analyses on 143 that were considered to be usable with regards to the supporting references (or using remarks provided by the three contributors that explained they collected an advance version compared to

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the reference). The difference between these two numbers was explained by the use of different currency units (meta-analysis based on models using wet weight, in t.km^{-2}, as currency units), or models not representing a whole ecosystem (e.g., only the pelagic part). Thus, 160 unique models (corresponding in reality to a higher number due to the duplicates) were not used in developed meta-analysis due to serious doubts on the quality of the model in comparison to the references. All these information were stored in EcoBase, so that a clear selection can be made in the future by other researchers. It could also enable to change this situation by updating corresponding Ecopath models.

An important step toward a better critical assessment of these models and a better collection of associated metadata (not all available in the supporting references, see Section 2.6) would be a back validation by models' authors. It would enable to clearly define a validated version of each model, along with changes compared to the supporting references, and thus to update EcoBase. This task can only be done through the ERDC that has the legitimacy and the scientific experience to organize it. A model repository working group was created, and EcoBase is a part of it. This model repository and the analyses developed in this thesis will be presented at the next 'EwE 30 years conference' and at the general assembly of the ERDC organized before the conference. This will be the occasion to give rise to a debate, and define a clear team methodology to achieve for each model a validation by the author, and the collection or update of associated metadata. Furthermore, this will be the occasion to ask for open-access authorization to enable each scientist to download or access models for reuse (see Chapter 2).

All these elements would enable to transparently select EwE models given precise quality criteria that can be estimated from EcoBase (see Sections 2.6, 5.5, and Appendix A). In fact, differences with supporting references are yet poorly explained, and need to be elucidated to

perform powerful meta-analysis. This could also enable to redevelop or update Ecopath models developed in the past. Furthermore, this would enable to develop or apply new techniques to select EwE models. In fact, quality and structure are important aspect to consider when performing meta-analyses (see Section 5.5.2). Several tools have been developed to quantitatively assess the quality of Ecopath models: the Pedigree index (Morissette, 2007), or the "DataReli" toolbox (Lassalle et al., 2014). However, it is yet few used and accounted for in meta-analyses. Interesting aspects could also be the development of new measures that can help categorizing and ranking models in classes for particular uses. In fact, Ecopath models can be built for different reasons with focus on particular ecosystem components, and possible new indices could focus on the completeness in the food web representation. Including such improvements in EcoBase and associated meta-analyses could enable a better selection of Ecopath models, and thus better analyses of general patterns in EwE models. Furthermore, it could enable to develop new analyses with clear selection criteria and associated research objectives. Finally, EcoBase does not consider Ecosim and Ecospace additional models. It would be interesting to develop the information repository so that it accounts for such important derived models.

6.2   Use of the EcoTroph model

EcoTroph is still a relatively recent approach that has yet still been few applied (see Section 2.5.1). However, it shows interesting insights into aquatic ecosystem trophic functioning. It enables a comparison of EwE models through a uniform framework, i.e., the trophic spectrum, and the calculation of several trophic indices useful for ecosystem-based management. The computation of trophic spectra is done using a smooth function (see Appendix B). Several

possibilities are implemented in EcoTroph to define this smooth function, and the general shape has been mostly developed through expert knowledge. Some critical assessments have been made to compare the different methods for building trophic spectra (Gasche et al., 2012; Libralato and Solidoro, 2010). Libralato and Solidoro (2010) notably showed that the shape of the smooth function can determine different estimated trophic indices, as well as changes in estimated transfer efficiencies. They concluded that using a normal distribution seemed to be the most reliable method. The current version of EcoTroph assumes a lognormal distribution. However, the sensitivity of such a distribution has been tested, and it showed that EcoTroph results were few sensitive to changes in determining parameters (see Gasche et al., 2012). An interesting improvement to the smooth function could be the validation by looking at the variability of TL of different species to validate the lognormal distribution and provide a statistical assessment. Initially, default values of the smooth function were defined using the empirical distribution of TLs observed by Chassot et al. (2008) for four species of the Celtic sea. However, few data are available to perform such an analysis for other species. In fact, it requires a large sampling of stomach contents to gain knowledge not only on aquatic species' diets, but also on their variability in time and space. This constitutes also a drawback of the Ecopath modelling approach, where a precise diet matrix is needed to balance the model.

Regarding the simulation procedure, ET-Diagnosis is based on a view of the food web as a biomass flow surging up the food webs. This general procedure is done assuming equilibrium, and does not consider time step. Furthermore, μ (the natural loss rate, see Eq. (3.7)) is considered to be constant. This constitutes a strong hypothesis, especially as it has been shown that it can change considering fishing impacts (Coll et al., 2009). This is partially corrected using the foraging arena equation (see Chapter 3). However, it would be interesting to assess changes in μ

due to fishing impacts, and consequently in the associated net transfer efficiencies. No general theory has yet been proposed or validated considering these possible changes; it seems that transfer efficiencies increase with a higher fishing pressure (Coll et al., 2009). Thus, it would be interesting to develop a new formulation taking into account fishing impacts on the μ parameter. This could notably be done by comparing EwE and EcoTroph results. Furthermore, more analyses are needed to better assess reliable values for this parameter. In fact, a mean value of 10% was used in analyses developed in the Chapter 3. However, different values were found by performing a meta-analysis of Ecopath models taking into account different ecosystem types and TL ranges (see Chapter 5).

Finally, we did not study impacts of the ɣ parameter integrated in the top-down equation and EcoTroph simulations (default value of 0.5; Eq. (3.11)). Thus, further work is needed to better assess the sensitivity of EcoTroph predictions to the input parameters. The different EcoTroph parameters could also be related to ecosystem traits, such as the ecosystem type. An interesting addition to the current EcoTroph package could be the development of an improved version of the ET-Dynamic procedure (Gascuel et al., 2009b; Gascuel and Pauly, 2009). This routine is a dynamic version of EcoTroph, which calculates differences in trophic spectra and associated parameters at each time step. These developments call for an extension of Chapter 3 analyses integrating more EwE models, TL-varying EcoTroph parameters, and ET-Dynamic simulations. Overall, EcoTroph constitutes a very useful and comprehensive model that still needs to be further developed and applied to better apprehend parameters' sensitivity.

6.3   Using new estimates and methods to perform a global mapping of the fishing impact

Results obtained in Chapter 5 indicated statistical differences between ecosystem types. These differences were focusing on trophic spectra and associated trophic functioning key parameters. Results enabled to provide new NTEs estimates for different TL ranges, which were different from previous estimates. Overall, two important parameters have been detailed: NTEs and kinetics. These two parameters were used in a previous work by Tremblay-Boyer et al. (2011) to provide a global mapping of fish biomass in the world ocean from 1950 to 2006. The methodology was based on the EcoTroph Catch Trophic Spectrum Analysis (CTSA; not used in this thesis). The CTSA is based on EcoTroph key ideas and equations. It uses a reverse formulation compared to the ET-Diagnosis routine enabling to calculate the biomass in an ecosystem based on primary production (PP), net transfer efficiency (NTE), sea surface temperature (SST; used to calculate the associated kinetic using a model developed by Gascuel et al. (2008)) and catch data by TL class (Figure 6.1). An interesting perspective would be to update this global mapping by updating associated parameters with news estimates. In fact, previous results covered the period 1950−2006 with a temporal resolution of decades. The major assumptions were: no dispersal of production between cells, spatial trends in the effects of fishing unaffected by temporal trends in primary production and sea surface temperature, net transfer efficiency constant over TL classes, time and space, and the biomass of predators not affected by top-down effects (Tremblay-Boyer et al., 2011).
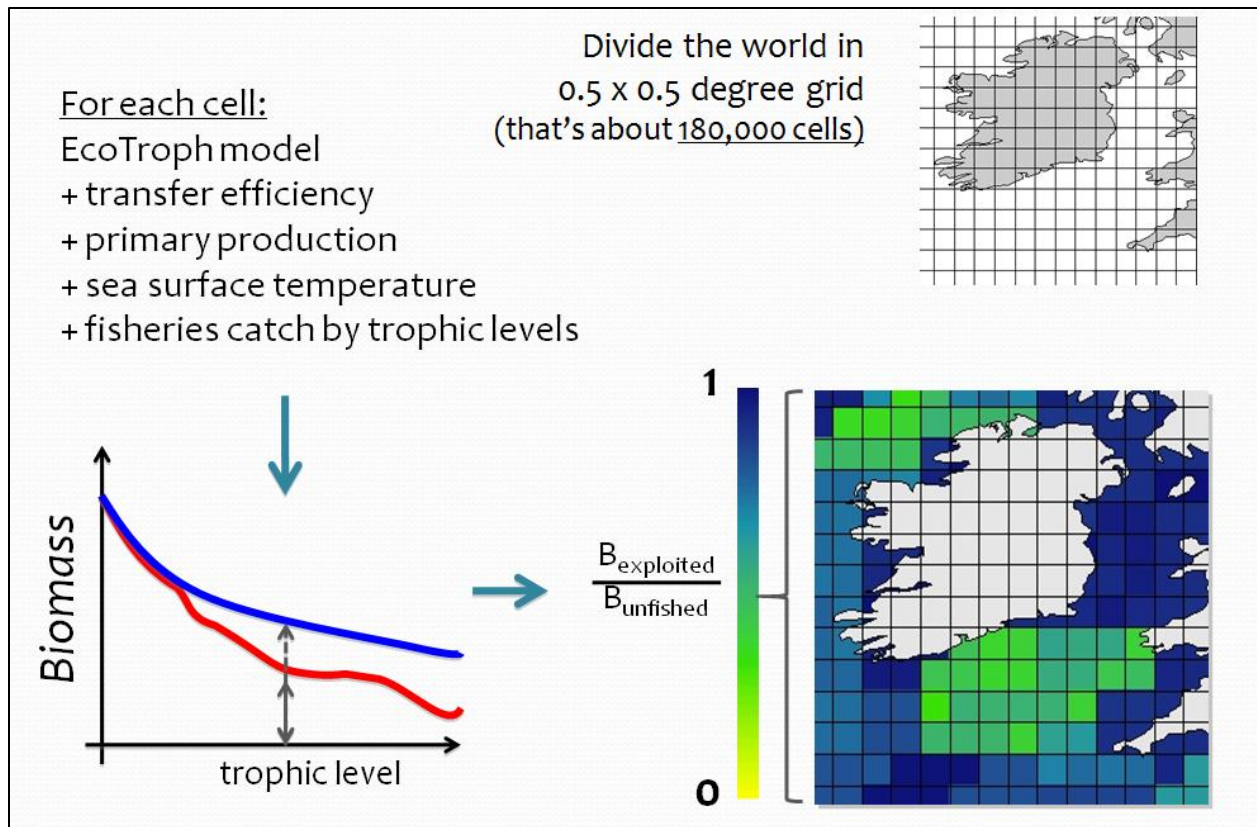
Figure 6.1 Methodology used in each ocean cell to estimate the fish biomass (from Tremblay-Boyer et al. (2011)).

A new analysis of the fishing impact from 1950 to 2010 could be carried out. A revised ET CTSA accounting for top-down and foraging arena controls could be applied to the 180 000 world ocean cells (0.5*0.5 degree cells). Furthermore, differences in trophic functioning between the cells could be considered thanks to the EwE models meta-analysis (Chapter 5), that is: ecosystem type key parameters, key parameters functions. Instead of using a net transfer efficiency constant over TL, time, and space (a 10% value was used), differential NTEs calculated for each cell could be used. This can be done by assigning to each cell an ecosystem type and the associated net transfer efficiencies. New mean KTS were also estimated, which could be used in the analysis (or potential new relation derived from the analysis of the natural

mortality, see Section 5.5). Furthermore, more accurate catch data were estimated by the SAUP based on FAO catch data reconstructions by country EEZ. These catch data, estimated from 1950 to 2010, will be allocated to each cell and used by the ET CTSA. Impacts of global warming could also be considered considering changes in primary production and sea surface temperature. In fact, SST variations could impact ET simulations, since it can be used as an input parameter. SST potentially affects kinetic relations intervening in ET equations. Primary production data are also input parameters determining trophic dynamics. Changes in PP could strongly affect ET simulation. Several models have been developed to predict SST and PP variations under climate change, and the method proposed by Cheung et al. (2010) could be used. They predicted PP and SST at the world scale from 2001 to 2060 using global circulation models, empirical models and algorithms (Delworth et al., 2006; Sarmiento et al., 2004). This would enable to develop a dynamic mapping of the climate impact on biomass from 2010 to 2060, perform sensitivity testing on the different parameters and assess potential biomass and trophic functioning changes. Other impacts of climate change (see Section 1.3) are difficult to account for by limited input data and equations. In such an approach, the knowledge gained through analyses developed in this thesis would be extrapolated to the world ocean providing a global overview of fishing impacts on marine ecosystems.

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Appendices

Appendix A EcoBase: a repository solution to gather and communicate information from EwE models

A.1   EcoBase description

- History

Sharing data among EwE developers has been a persistent dream, and a model depository was implemented on the Ecopath website (http://www.ecopath.org). However, only a small fraction of the published models were included on the web-page, and the structure was not in place for extensive data sharing. That is the reason why the idea of creating a new models repository has been growing since the creation of the Ecopath Research and Development Consortium (ERDC). The EcoBase project itself started with my PhD project, which consists in a meta-analysis of EwE models focusing on the trophic functioning of aquatic ecosystems. First, EwE models coming from two existing databases were gathered:

- Dr. Lyne Morissette developed Excel sheets for 178 EwE models, and listed the total number of EwE models developed to date (393 models; Morissette, 2007). She collected some metadata (publication year, reference, ecosystem type, area, modeled period, Ecosim model developed), as well as detailed data on each of the 178 EwE models (main inputs and outputs);

- Drs. Luís Antonio Salcido-Guevara and Francisco Arreguín-Sánchez developed an Access database, called ECOMOD, accounting for 153 models. This database was

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initiated during the INCOFISH project (http://www.incofish.org/), and expanded later on as part of Dr. Salcido-Guevara PhD project (Salcido Guevara, 2006). The database integrated several metadata (publication info, geographic location, country, FAO area, LME, ecosystem type, etc.), functional groups, and all input and output data (basic parameterization and network analysis). All models were updated to EwE version 5.1 and verified in respect to associated publications.

The first step was then to compare and merge both sets of EwE models into one single database supported by PostgreSQL to create a data server. Making the same data available all over the world from a single database is the first step for information sharing. The main challenge was to define a database structure accounting for all compatibility and identification issues. Notably, duplicates were double-checked, as the versions of similar EwE models inherited from both collections to be identical. Indeed, some models had been modified to be balanced if they were not, whereas others were still not balanced. However, most of the time, all the modifications had been recorded and the collections proved to be very valuable materials. The two existing databases both integrated the great collection of documentation and files listed in the Ecopath website. After matching, a list of about 200 unique models was obtained. Then, a third contribution was added to EcoBase: Dr. Villy Christensen and his team had gathered a collection of 233 EwE models, with their associated publications. Some metadata about the person through whom the model was given and the few modifications made had also been recorded. This collection was compared and merged as well to the previous list. An additional list of 132 unique additional models was obtained after comparison. Several authors have also sent their models directly for incorporation in the repository. Finally, since the inherited collections were not up-to-date with the most recent EwE models published, Audrey Valls and I

conducted a literature review and ended up with a list of 99 recent (or previously missing) models, to be added to the list. Thus, a final list of 435 unique models and 563 models in total (including duplicates) was obtained. A list of the EwE models registered and referenced in EcoBase is provided on the EcoBase website (http://sirs.agrocampus-ouest.fr/EcoBase/; with details on the model location, period, country, author, and reference).

- Software and access

Several database management systems were available to develop the information repository. The PostgreSQL software was chosen to be used. PostgreSQL is a professional relational database management system. It is a free software, and sources are available (http://www.postgresql.org/). All its technical capabilities make it a robust and widely used management system. It notably has graphical interfaces to manage tables, libraries for various programming languages, and drivers for the Microsoft Open Database Connectivity (ODBC) application programming interface (API) enabling connections with several softwares. The database server is currently hosted on a development server at Agrocampus Ouest (Rennes, France) and accessible everywhere in the world (with access authorization).

Currently, access to the repository is possible through various interfaces such as: pgAdmin "the most popular and feature rich Open Source administration and development platform for PostgreSQL, the most advanced Open Source database in the world" (http://www.pgadmin.org/), any Internet server, or Microsoft Access (http://office.microsoft.com/en-ca/) through ODBC connections. All the different ways to access the repository are currently restricted with user logins and passwords, managed by the database administrators (DBAs). Full access to the repository is restricted to expert users (EUs) only.

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However, a large number of web services may become accessible to general users (GUs) (see Section A.2).

- Structure of the repository

EcoBase comprises numerous tables encompassing all Ecopath data and various metadata. The architecture of the repository relies on one main table called 'models_list'. This table is used to declare all encoded models by assigning a unique number to each one, declared as a primary key: the 'model_number' variable. A primary key is a special relational database table column (or combination of columns) designated to uniquely identify all table records. It must contain a unique value for each row of data and no null values. The 'model_number' primary key enables a complete identification of each single model and linkages to other tables comprising the other data. Along with 'models_list', four other tables ('references_tables', 'models_details', 'fishery_fleets', and 'import_like_groups') are used to declare the four other primary keys needed to create the linked tables (Figure A.1). All five tables enable the creation of a series of tables used to store all the other data. Three categories of data stored in EcoBase were differentiated.

A first objective of this approach was to store metadata on EwE models. These data are necessary for a complete identification of each model and to provide information not directly included in EwE data, such as the location of the ecosystem, the objectives and history of the model or its contributors. The definition of metadata was based on potential needs for conducting meta-analyses, and key points identified by merging the three existing databases of EwE models. All metadata were stored in five tables (Figure A.2). Three additional tables linked with 'models_list' were created: 'models_history', 'models_info' and 'models_ref' (also linked with

'references_table'). Jointly, these tables enable a complete storage of all metadata and models quality criteria. A comprehensive list and detailed description of all the models' metadata fields is available in Colléter et al. (2013b).
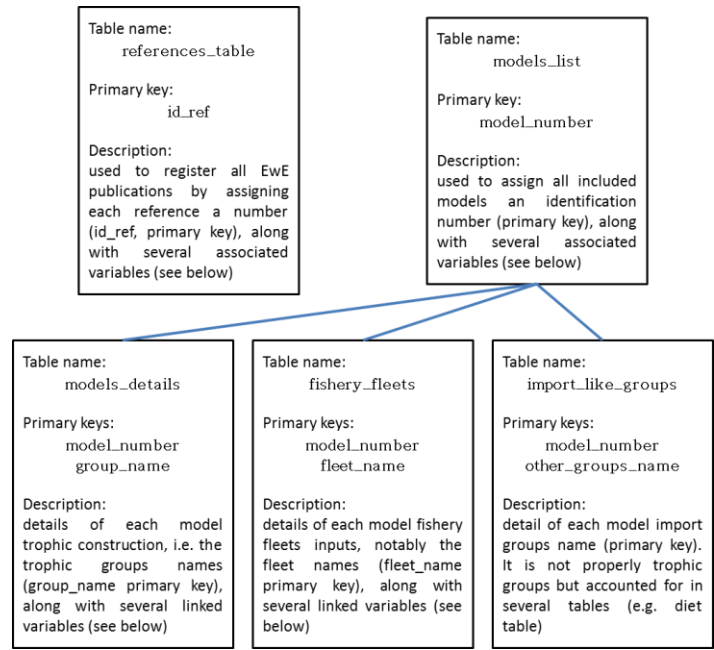
Figure A.1 Basic diagram of the five main tables of the PostgreSQL EcoBase repository (name of the tables, associated primary keys and a short description).
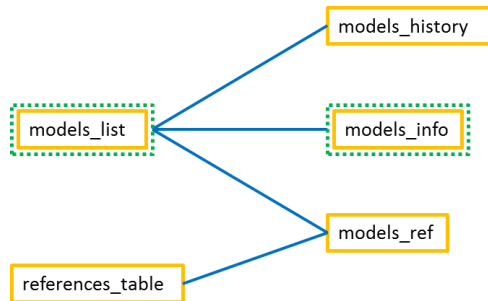
Figure A.2 Relation diagram of the five metadata tables (orange solid contours indicate tables containing metadata, green dotted ones tables containing EwE inputs).

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The descriptive data required to build EwE models were also stored, here called 'model inputs'. Several tables have been designed to store these data (Figure A.3). The names of the tables and fields have been designed to enable an easy understanding, and to create a homogeneous database with condensed information. All tables rely on the 'models_list' table and the three main associated tables 'models_details', 'fishery_fleets' and 'import_like_groups'. This ensures referential integrity of EcoBase (e.g., if a model is suppressed from models_ list, then all associated records are suppressed too). The repository has been designed to store all the input data coming from EwE version 6.3, also accounting for additional routines like the Taxonomy or Pedigree (Figure A.4). An exhaustive list and detailed description of all models' inputs fields is available in Colléter et al. (2013b).
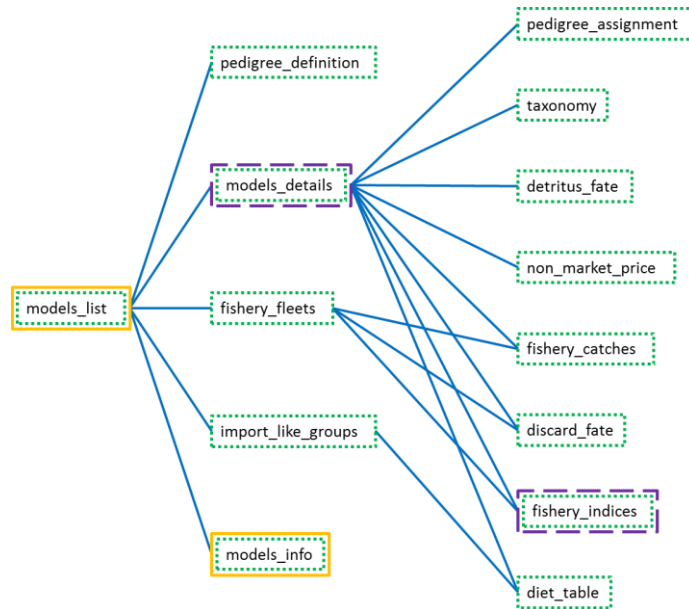
Figure A.3 Relation diagram of the EwE input tables (orange solid contours indicate tables containing metadata, green dotted ones tables containing EwE inputs, and purple dashed ones tables containing EwE outputs).
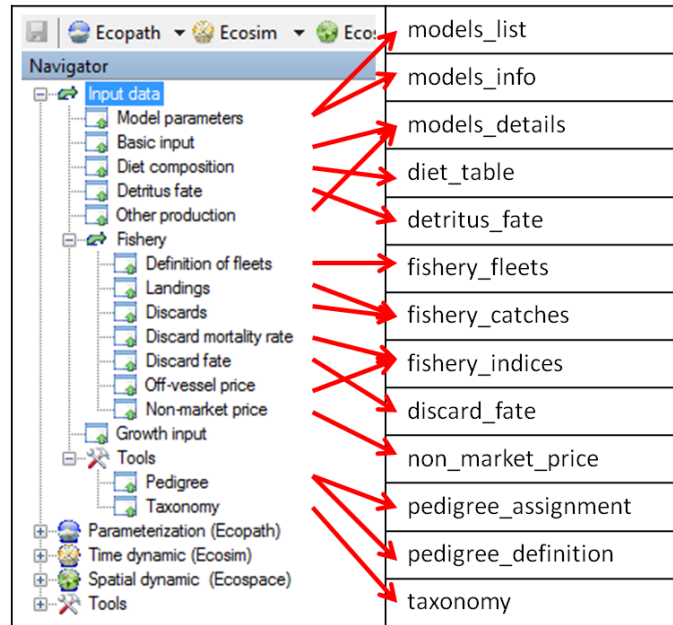
Figure A.4 Snapshot of EwE software navigator for input data, and correspondence with EcoBase tables.

For the purpose of analyses presented in this thesis, the computed data obtained from EwE models were stored in EcoBase as well (the Ecopath routine only), here called 'model outputs'. In fact, several outputs are needed to perform meta-analyses or run EwE plug-ins, such as EcoTroph. Again, several tables have been designed to store these data (Figure A.5). As for the 'model inputs', the tables and fields names have been chosen to simplify the usage and structure of EcoBase. The referential integrity is guaranteed by relations between tables and the use of the four main tables: 'models_list', 'models_details', 'fishery_fleets' and 'import_like_groups'.

The repository has been designed to store output data coming from EwE version 6.3 (Figure A.6 and Figure A.7). The Fishery Quantity and Value tables and the Relative Flows table were not considered as they are easily computable with included data. Details of the Cycle and Pathways module are not yet accounted for, due to the large amount of data this would have

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required, and neither are the Ecosim Network Analysis and Value Chain modules. The architecture of EcoBase can still evolve to include new data and fulfill new needs expressed by the EwE community. A complete list and full description of all the models' outputs fields is available in Colléter et al. (2013b).

In conclusion, EcoBase has been designed to store almost all data coming from EwE version 6.3, also accounting for several relevant modules, such as the Taxonomy, Particle Size Distribution and Pedigree. Additional metadata may also be stored, such as the geographic coordinates (spatial extent of the model; see Colléter et al., 2013b). Model quality criteria were also added for selection and meta-analyses. The entire structure of EcoBase can be summarized using a relations diagram (Figure A.8). The chosen format is suitable not only for the particular use required in this thesis, but also for a global use by any EwE modelers and fisheries scientists.
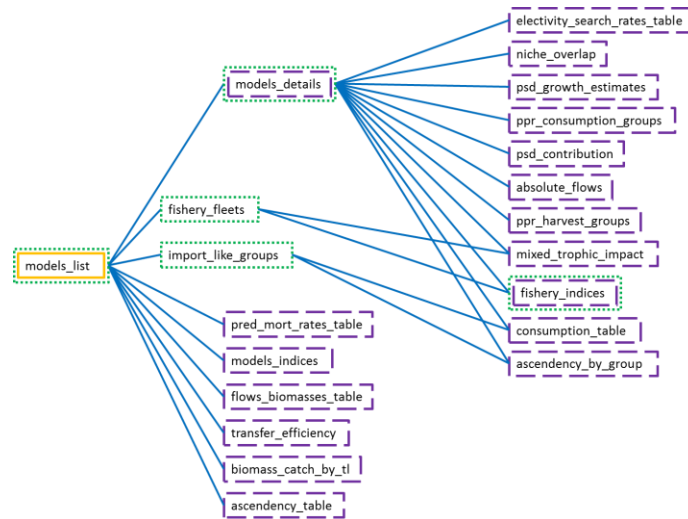
Figure A.5 Relation diagram of the EwE input tables (orange solid contours indicate tables containing metadata, green dotted ones tables containing EwE inputs, and purple dashed ones tables containing EwE outputs).
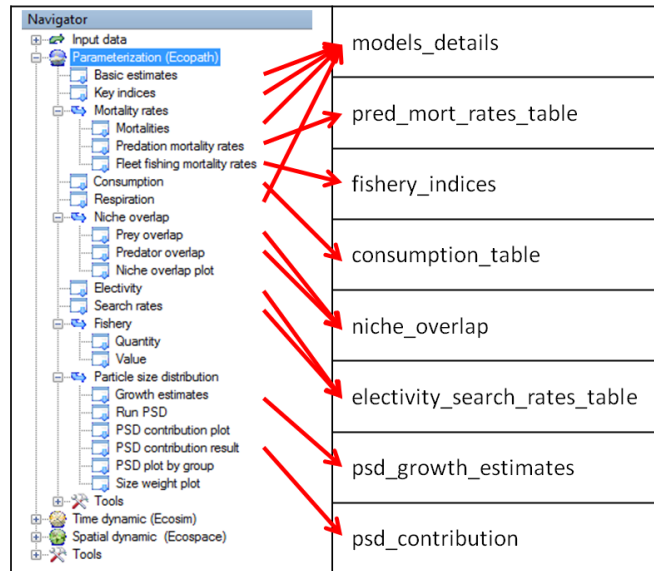
Figure A.6 Snapshot of EwE software navigator for output data, and correspondence with EcoBase tables.
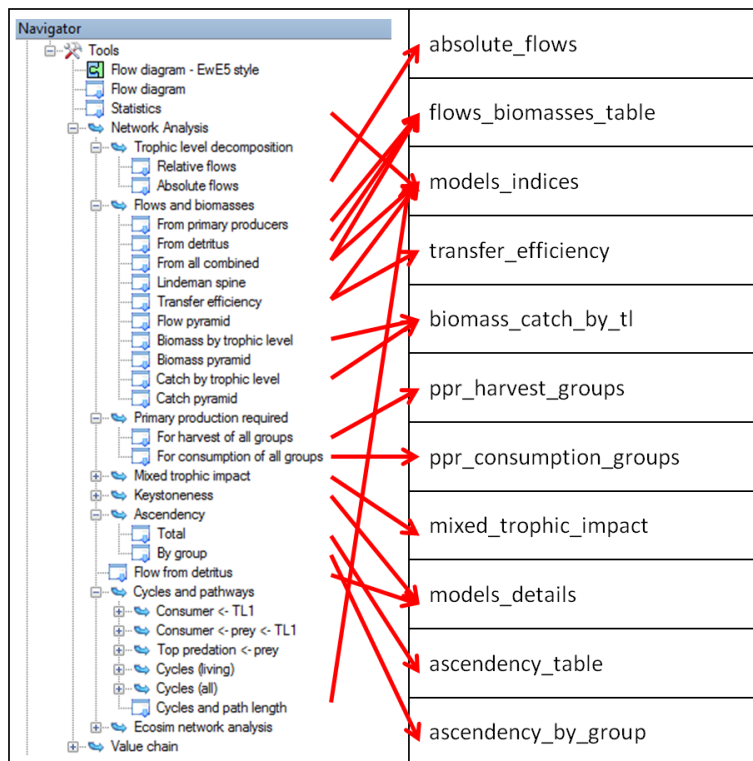
Figure A.7 Snapshot of EwE software navigator for Network analysis output data, and correspondence with EcoBase tables.
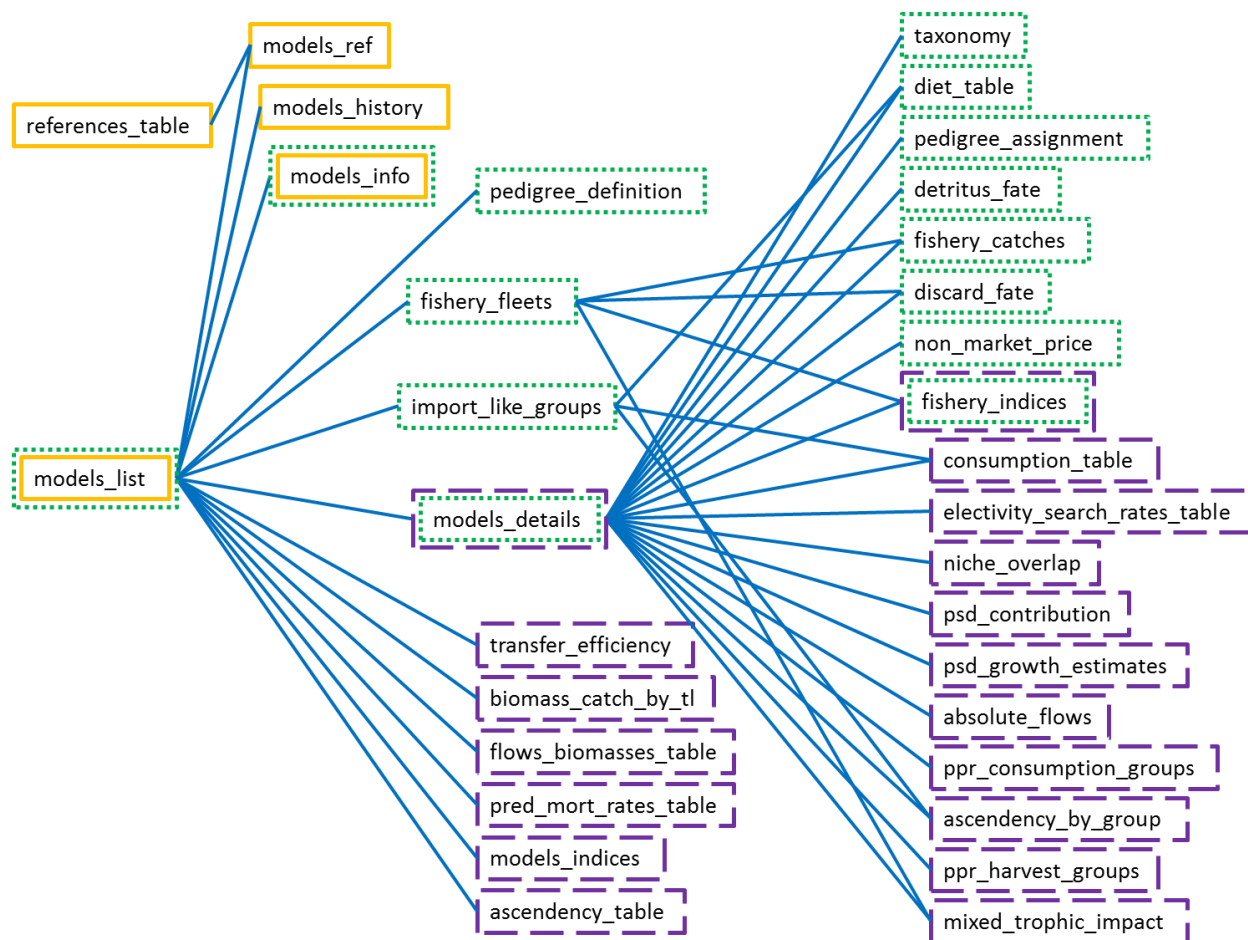
Figure A.8 Diagram of tables relations (orange solid contours indicate tables containing metadata, green dotted ones tables containing EwE inputs, and purple dashed ones tables containing EwE outputs).

A.2   EcoBase capabilities

- Overview

After presenting the repository software and structure, the possible usages of EcoBase are introduced in this section, as well as functionalities associated to the different users categories: the general users, and the developers including the database administrators (DBAs) and the

expert users. The PostgreSQL Relational Database Management System (RDBMS) and the structure we developed enable powerful capabilities to share services linked with the database content. As for the database administrators, the EcoBase RDBMS and structure present interesting capabilities such as: a control of the access, centralized modifications, and a unique information source. DBAs as well as EUs can directly use the database to manage structure and access, or perform analyses. Such powerful capabilities cannot logically be given to everybody. GUs need more elaborated and controlled pathways to access data, via web services (Figure A.9). Once users' needs are expressed, we have to deal with three main issues: (i) how to organize the database feeding; (ii) how to disseminate the data; (iii) which services to set up.
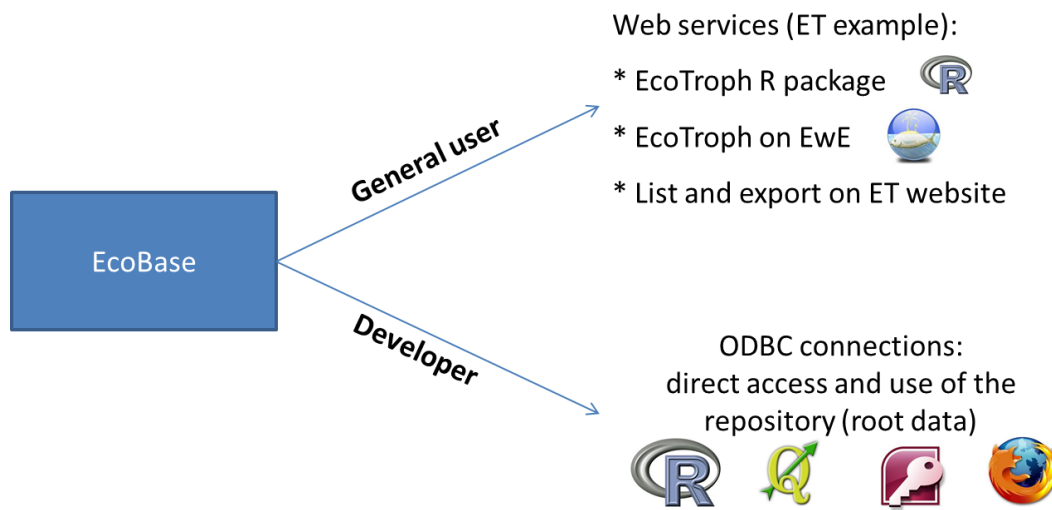
Figure A.9 PostgreSQL formats user's functionalities.

- For general users

A great number of web services responding to the GUs' expectations are possible using EwE models data loaded in EcoBase and metadata added for each model. Examples detailed

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below focus on web services already developed and related to the EcoTroph approach, which give an interesting overview of the potential capabilities of EcoBase.

- EcoTroph R package: An EcoTroph R package has been developed enabling an independent use of the EcoTroph model (Appendix B; Colléter et al., 2013a). This package contains EcoTroph functions but also a 'read.ecopath.model' function. This function enables the loading of data needed for EcoTroph analyses from each model in EcoBase with a granted access. EcoTroph users are given the possibility to analyze any Ecopath model available in the EcoBase models repository.

- EwE EcoTroph plug-in: A new functionality of the EwE EcoTroph plug-in is a linkage with EcoBase. EcoTroph inputs can be loaded in three different ways: from the model loaded in EwE, from an external .xml file, or from EcoBase via a web service which lists each model in EcoBase with a granted access and downloads the selected one.

A list of available EwE models stored in the repository and a short description of each of them is displayed on the EcoBase website (http://sirs.agrocampus-ouest.fr/EcoBase/). Users have the possibility to select a model, obtain additional information and see a map of the spatial extent of the model. Data needed for EcoTroph are also downloadable from this interface for each model in EcoBase with a granted access. The web service is yet limited (search by name or on a map if the geographic extent of the model is known), but advanced search capabilities could be easily developed using the models' metadata.

- For developers only

EcoBase presents great capabilities for developers (including DBAs and EUs). First, a full control of the access to root data (tables and structure) is possible through security features

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of PostgreSQL (controlled by login, password, IP). Expert users who want to connect directly to the database need a user login and a password controlled by database administrators. There is also the possibility to manage different rights to users (data consulting only, data editing, etc.). Expert users can access to the complete database through the use of ODBC connections or the web interface, with clearly defined access rights allocated by database administrators. This opens new capabilities for expert users, notably statistical analyses using R and the package RODBC (http://cran.r-project.org/web/packages/RODBC/index.html) (or Rpgsql for Linux users), or spatial outputs using GIS tools. The great amount of data and the easy access through R is an open gate to large and reproducible analyses. However, these expert users' capabilities do not constitute the standard way to use the database, since it is often the less controlled and more CPU time-consuming. Thus, the number of expert users should be limited to ensure that standard services will always be available for general users.

In conclusion, EcoBase constitutes a unique source of information where modifications and usages are centralized and manageable. Access is possible all over the world, freely and easily. The repository can be managed by several database administrators at different places, and enables the set-up of a developers' community. Data access is fully controlled by database administrators through the use of clearly defined rights to the associated expert users, and web services for general users. A great number of web services answering general users' expectations are possible using EwE models data loaded in EcoBase and metadata added for each model. Provided examples concentrate on EcoTroph use, but give an interesting overview of capabilities. Direct interactions with the EwE software are possible, as external uses to provide additional information.

A.3 EcoBase current state and future developments

- Current state of EcoBase

As presented in the sections above, the core structure of EcoBase is in place but not all the fields have been encoded yet. Thus, in its current state, the models repository is not completed. The first phase of encoding focused on metadata. An exhaustive inventory of all published EwE models was completed and a final list of models in EcoBase was established. For all listed models, available information on metadata was then collected from the original publications describing the models and encoding of all fields consisting in metadata was completed. However, few actual data has been encoded in EcoBase yet. 563 EwE models are currently referenced in the EcoBase repository of which 435 are unique. Table A.1 shows a detailed assessment of the current data availability, by table and for all referenced models. Data used by the EcoTroph routines have been encoded, as part of this thesis, for all models coming from the three contributors' databases. The completion of encoding will constitute the second phase of the project. EcoBase structure enables encoding of all input or output data from any referenced Ecopath models. EcoBase originally focused on the Ecopath routine of EwE models, so that no Ecosim time series or Ecospace maps can be stored in the database in its current state. Also, EwE scenarios are a type of data highly dependent on the context in which they were generated, putting restrictions on their potential reuse.

Table A.1 Data availability for all referenced models in EcoBase (September 2014).

Table	Data type	Data availability
absolute_flows	Output	Empty
ascendency_by_group	Output	Column 'Throughput' available for models initially

Table	Data type	Data availability
		assembled by L. Morissette and F. Arreguín-Sánchez
ascendency_table	Output	Empty
biomass_catch_by_tl	Output	Empty
consumption_table	Output	Empty
detritus_fate	Input	Available for one model (test)
diet_table	Input	Available for one model (test)
discard_fate	Input	Available for one model (test)
electivity_search_rates_table	Output	Empty
fishery_catches	Input	Available for models assembled by the three contributors
fishery_fleets	Input	Available for models assembled by the three contributors
fishery_indices	Input/Output	Available for one model (test)
flows_biomasses_table	Output	Empty
mixed_trophic_impact	Output	Empty
models_details	Input/Output	Available for models assembled by the three contributors
models_history	Metadata	Available for all models
models_indices	Output	Available for models assembled by the three contributors
models_info	Metadata/Input	Available for all models
models_list	Metadata/Input	Available for all models
models_ref	Metadata	Available for all models
niche_overlap	Output	Empty
non_market_price	Input	Available for one model (test)
other_groups	Input	Available for models assembled by the three contributors
pedigree_assignment	Input	Empty
pedigree_definition	Input	Empty
ppr_consumption_groups	Output	Empty
ppr_harvest_groups	Output	Empty
pred_mort_rates_table	Output	Empty
psd_contribution	Output	Empty
psd_growth_estimates	Output	Empty
references_table	Metadata	Available for all recorded references
taxonomy	Input	Empty
transfer_efficiency	Output	Empty

- Future improvements of EcoBase

EcoBase is an on-going project and many features are still to be improved to make it a more powerful and efficient tool. Table A.2 shows a report card of EcoBase, which summarizes

the key features already implemented, or still to be implemented, and estimates the degree of completion of each feature. Future improvements should notably focus on data encoding, linkages between EcoBase and the EwE software and database access policy. Also, users should not be allowed to encode outputs which are not consistent with the inputs. Maintenance of EcoBase in the long-term is probably the most critical aspect to ensure a long life span of the repository, facing issues such as migration to new technologies or updating.

Table A.2 Report card of EcoBase.

	Feature	Grade	Comment
1	Structure	A	Structure is in place for storing metadata and Ecopath input/output data. Note: no Ecosim or Ecospace data considered yet.
2	Metadata	A	Metadata encoding is completed and metadata are accessible and usable. Remaining missing metadata was not provided in the references.
3	Data	D	Data encoding is not completed and data are not accessible or usable. Requires completion of items 4 and 5.
4	Links with the EwE software	C	No link between EcoBase and the EwE software is currently available, but feasible to develop such linkages. Several options are under consideration.
5	Open-access	C	Several options are under consideration. Requires a consensus within the ERDC.
6	Website and web services	B	Website partially completed: some functionalities already implemented such as models browser; some still missing such as fill-in forms for adding models.
7	Short-term maintenance	A	Mathieu Colléter and Jérôme Guitton are in charge of the maintenance in the short term.
8	Long-term maintenance	D	Modalities of the maintenance in the long-term still have to be defined.

- Projects possibly involving EcoBase

As mentioned in the Chapter 2, only a few meta-analyses based on a large collection of EwE models have been published. EcoBase creates new opportunities for various types of meta-analyses, involving larger datasets, at broader scales. The repository notably provides standardized and atomized metadata, which may be used as selection criteria. By applying a

scoring method on these criteria, a list of models of potential interest may be obtained. The pool of selected models may then be reused to conduct meta-analyses. Also, the ODBC connections and web services enable direct links between EcoBase and popular statistical softwares such as R (http://www.r-project.org/), which allows for statistical analyses to be easily and quickly run. Besides, new mapping tools for EwE models are available in EcoBase and may be used to get new insights on EwE-based research worldwide (see Chapter 2). Table A.3 shows a list of researchers who are members of on-going projects using EcoBase, or who have expressed strong interest in using the models repository. The list is not meant to be exhaustive and should grow as EcoBase is enhanced.

Table A.3 List of on-going and potential projects involving EcoBase.

Researcher	Interest	Project status
Mathieu Colléter (UBC/Agrocampus Ouest)	Trophic functioning meta-analysis (TE, Kinetic) and EcoTroph use	On-going PhD thesis
Audrey Valls (UBC, Nereus Program)	Index of Keystoneness; Diet composition	On-going PhD thesis
Sylvie Guénette (EcOceans)	Trophic role of small pelagics	Interests expressed
James Watson (Nereus Program)	Particle size distributions	Interests expressed
Deng Palomares (UBC, FishBase)	Links EcoBase-FishBase	Interests expressed
Jérôme Guitton (Agrocampus Ouest)	Links EcoBase-EwE	On-going project
Jérémy Lobry (IRSTEA)	Meta-analysis of EwE models of estuaries	Interests expressed
Jean Guillard, Orlanne Anneville, and Jérémy Lobry (INRA/IRSTEA)	Meta-analysis of EwE models of lakes (Alpes)	Interests expressed (PhD thesis)
James Simons (CCS-TAMU-CC)	Linking EcoBase with the Gulf of Mexico trophic database	Interests expressed (GoMexSI project)
Luis Salcido-Guevara (IPN-CICIMAR)	Supply-demand balance of trophic networks	On-going research
Francisco Arreguín-Sánchez (IPN-CICIMAR)	Ecosystem functional indicators	On-going research
Monica Ruiz-Barreiro (IPN-CICIMAR)	Exergy: application to management and conservation	Interests expressed (PhD thesis)

- Links with the Ecopath Research and Development Consortium

Building a models repository was an initiative of the Ecopath Research and Development Consortium (ERDC), and EcoBase is an outcome of this initiative. The EcoBase project was instigated with two main phases in mind. Phase 1 consisted in establishing an up-to-date and comprehensive list of published Ecopath models and making the models discoverable through an online repository. Phase 1 notably involved: (i) merging three pre-existing lists of Ecopath models, gathered by Francisco Arreguín-Sánchez, Lyne Morissette and Villy Christensen; (ii) selecting published Ecopath models only and identifying their associated references (citations); (iii) collecting metadata about the published Ecopath models, when provided in the associated references (Chapter 2). Phase 1 has been done as part of Mathieu Colléter and Audrey Valls' PhD theses and is now completed. It will be valuable to anyone willing to conduct meta-analyses of Ecopath models.

Phase 2 is meant to be taken over by the ERDC, under the coordination of the Models Repository Working Group. The ERDC was initiated in Vancouver, Canada, in October 2011, and formally established in Edinburgh, Scotland, in May 2012. It is "a global, cooperative network focused on the research, development and sustainability of the EwE approach and software, its information basis, and complementary activities and capabilities". Its objective is "to contribute to the sustainability of living resources and ecosystems by developing, applying, teaching, and promoting modeling and analytical tools, with a focus on the EwE modeling approach" (http://www.ecopath.org/consortium). Phase 2 will consist in making accessible to and reusable by the EwE community all the Ecopath models which are currently discoverable in EcoBase. Open-access has to become the way of thinking in ecology and the EcoBase repository

was built with this idea in mind. Thus, it is hoped that the ERDC will encourage the EwE community to take that route as well.

A.4   Conclusion

This appendix constituted a great opportunity to present the on-going EcoBase project. The EcoBase models repository is meant to make published EwE models discoverable, accessible and reusable, and thus to enhance the promotion of EwE-based approaches and meta-analyses in marine ecosystem modeling. It has been designed to meet global scientific challenges, such as data sharing, gathering and dissemination. Three existing EwE models databases were merged into a new models repository enabling more powerful capabilities. The architecture of EcoBase is meant to correspond to the EwE software structure (version 6.3) and collect all the data required for conducting meta-analyses and ensuring models identification. A large amount of metadata on the models origin, structure, and history were integrated, as well as the modeled ecosystems traits. Moreover, the PostgreSQL format enables new capabilities for data sharing and access control. The structure of the repository is flexible, and the database administrators have a full control on users' access. Thus, different user profiles are configurable through the use of web services. Interesting examples of web services linked with the EcoTroph approach have already been developed, and there are possibilities for more if new users are willing to develop their own tools in the future.

This appendix and the associated *Fisheries Centre Research Report* (Colléter et al., 2013b) represent the completion of the phase 1 of the EcoBase project. The models repository was developed as part of the ERDC initiative to move forward in EwE modeling. It is hoped that EcoBase will offer new functionalities to the EwE community and bring new perspectives within

the ERDC. The phase 2 of the EcoBase project is meant to be taken over by the members of the Models Repository Working Group, under the coordination of the ERDC. They should develop new linkages between EwE and EcoBase, which could help encoding all missing data in EcoBase as well as developing new web services for EwE modelers. The EcoBase project is a new opportunity for strengthening the EwE community via a shared online tool, and it offers new capabilities for EwE research and communication.

Appendix B An introduction to the EcoTroph R package: analyzing aquatic ecosystem trophic networks

B.1   Summary

Recent advances in aquatic ecosystem modeling have particularly focused on trophic network analysis through trophodynamic models. Here, a R package devoted to a recently developed model, EcoTroph, is presented. This model enables the analysis of aquatic ecological networks and the related impacts of fisheries. It was available through a plug-in in the well-known Ecopath with Ecosim software or through implementations in Excel sheets. The R package simplifies the access to the EcoTroph model and offers a new interfacing between two widely used software, Ecopath and R.

B.2   Introduction

In the face of the global overexploitation of marine resources and the fast degradation of ecosystems integrity, scientists developed new modeling approaches at the scale of the ecosystem. In fact, the main tool used for fisheries regulation is a stock approach which does not account for the trophic network linking marine ecological components. An important challenge is to analyze the aquatic ecological networks and the related impacts of fishery. There are several ways to define and represent an ecosystem. One widely used approach is based on the trophic level concept. Elton (1927) and Lindeman (1942) introduced this concept for describing aquatic ecosystems by assigning integer trophic levels to the individual numbers, to the biomass or to the biological production by its component species. This approach differentiated between primary producers and detritus (TL=1), first-order consumers (TL=2), second-order consumers (TL=3)…

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The ecosystem is so represented as a pyramid of number, biomass or production, from low to high TLs. Odum and Heald (1975) developed this concept by implementing fractional trophic levels resulting from the diet of the individual and the trophic level of its preys. The emergence of Ecopath as a widely used approach and software for modeling aquatic ecosystems (Christensen and Pauly, 1992; Polovina, 1984) contributed in a major way to the prominence of TLs, especially as they were not an input, but an output of the model (i.e. estimated parameters). As the use of Ecopath spread worldwide with hundreds of application cases, so did the trophic level concept.

EcoTroph is an approach and software for modeling marine and freshwater ecosystems, entirely articulated around the TL concept (Gascuel, 2005; Gascuel and Pauly, 2009). It has been developed at the same time as the Ecopath worldwide expansion happened and incorporated into the Ecopath plug-in family (Gascuel et al., 2009b). The first key idea of ET is that it deals with the continuous distribution of the biomass in an ecosystem as a function of continuous TL. The biomass enters the food web at TL=1, generated by the photosynthetic activity of primary producers, or recycled from the detritus by the microbial loop. Between TL=1 and TL=2, the biomass is composed of mixotrophs only, and is usually low. If any, it is conventionally split between biomasses at TL=1 and 2. Then, at TLs≥2, the biomass is composed by heterotrophic organisms with mixed diet and fractional TLs resulting in a continuous distribution of biomass along TLs. The second key feature of ET is that the trophic functioning of aquatic ecosystems is modeled as a continuous flow of biomass surging up the food web, from lower to higher TLs, through predation and ontogenic processes. All the equations of the model are detailed in Section 3.3 and Gascuel et al. (2011). Such an approach, wherein species as such disappear, may be viewed as the final stage in the use of the TL metric for ecosystem modeling. It provides a

simplified but useful representation of ecosystem functioning and impacts of fishing. ET has been used either in theoretical contexts based on virtual ecosystems (Gascuel et al., 2011; Gascuel and Pauly, 2009), or in specific case studies to assess the current fishing impacts at the ecosystem scale in the South African Benguela ecosystem (Gasche et al., 2012), in the Bay of Biscay (Lassalle et al., 2012), for a worldwide analysis (Tremblay-Boyer et al., 2011), or to analyze the effects of marine protected areas on the whole food web (Senegal, Colléter et al., 2012; Mediterranean Sea, Valls et al., 2012). Furthermore, ET enables the construction of a unique comparison framework for Ecopath models, the trophic spectrum. This display, based on ET key ideas, is a graphical representation of the ecosystem parameters, such as biomass, production, catch, fishing mortality, etc., along the trophic level (Gascuel et al., 2005).

This package is the first attempt to offer interfacing between R and Ecopath through its plug-in EcoTroph. The plug-in will use R and the EcoTroph package within the free Ecopath with Ecosim software. This enables the use of ET for a large panel through the plug-in for inexperienced R users, or directly the R package for the more expert ones. On the developer side, this way to link a rich user interface (developed in Microsoft VB) and a well-known software in the fishery scientists group such as R is a way to set up a community. These researchers can so focus on the model improvements without taking into account the rich user interface which is time consuming. Along with several functions, an example dataset on the Guinean marine ecosystem (Gascuel et al., 2009a) was included within the package. This article introduces, using the example dataset, the three main components of EcoTroph:

- The data import and validation

- The ET-Transpose tool

- The ET-Diagnosis tool

A great deal of documentation, both introductory and advanced, is available on the ET website (http://sirs.agrocampus-ouest.fr/EcoTroph). The EcoTroph package requires the XML package (Lang, 2012) in order to load the model input parameters coming from the Ecopath software. The read.ecopath.model function will parse the data.

B.3   Data import and validation

The EcoTroph package requires an input data table to run. The user has to load this dataset under the different possible formats ('.xls', '.csv', '.txt') with the functions read.table, read.csv… The ecopath_guinee dataset (Table B.1) is an example of a suitable input table constructed for use with the EcoTroph package.

Table B.1 Data from the Ecopath model of the Guinean ecosystem (extracts).

	group_name	TL	biomass	prod	catch.1	catch.2	accessibility	OI
1	Whales	4.01	0.0309	0.020	0.000	0.000	0.0	0.059
2	Dolphins	4.48	0.0433	0.070	0.000	0.000	0.0	0.331
3	Turtles	2.19	0.0296	0.150	0.000	0.000	0.0	0.338
4	Sea birds	3.81	0.0013	0.300	0.000	0.000	0.0	0.353
5	Rays+	3.97	0.3860	0.363	0.012	0.024	0.9	0.329
6	Sharks+	4.31	0.1050	0.410	0.007	0.003	0.8	0.633
7	Large pelagics	4.21	0.3840	0.850	0.025	0.069	0.8	0.263
8	Barracudas+	4.12	0.0583	0.920	0.009	0.022	0.9	0.259
9	Carangids	4.16	0.0627	1.000	0.010	0.024	0.8	0.139
10	Horse Makerels+	3.13	2.3330	0.700	0.000	0.115	0.8	0.366
…	…	…	…	…	…	…	…	…
34	Primary producers	1	69.0000	84.000	0.000	0.000	0.0	0.000
35	Detritus	1	290.0000	0.000	0.000	0.000	0.0	0.193

The variable names have to be specified and strictly the same as above: group_name (name of the group representing one or several species gathered together), TL (the trophic level of

the group), biomass (the biomass of the group), prod (the production on biomass ratio or P/B) and accessibility (the ratio of the group biomass that would be caught assuming an infinite fishing pressure). These parameters generally come from Ecopath inputs or outputs, but can also be independent. The entry catch.1, catch.2, catch.whatyouwant is necessary if several fisheries do exist. The OI column (the omnivory index, an Ecopath output parameter) is optional, it is used in the create.smooth function for an alternative smooth form (sigmaLN=OI/TL$_j$, see below).

The check.table function was developed to check the compatibility of the input data table with the EcoTroph package:

```
check.table(ecopath_guinee)
```

In the example, no warning message appears as no error is made. If a message appears, the user has to correct the dataset in view of the comments. No missing values (NAs) are accepted as input, a yield column has to be entered with 0-values if no catches are registered. As well as the yield, the P/B of detritus groups (not entered in Ecopath) has to be set to 0. The check.table function converts the input dataset into a 'data.frame' object if it is not already one.

A read.ecopath.model function was also implemented. It allows users to import data in '.xml' format exported from the Ecopath/EcoTroph plug-in or distributed by a web service (a database of Ecopath models has been set up to allow a meta-analysis at a world scale, http://sirs.agrocampus-ouest.fr/EcoBase). This function formats the inputs so they meet the EcoTroph package requirements. Nevertheless, it is advisable to check the data consistency using the check.table function.

B.4   ET-Transpose tool

- Creation of the Smooth function

The Smooth function returns a table allowing the conversion of data referring to specific taxons or functional groups (Ecopath trophic groups for example) into data referring to trophic classes. The major assumption of this function is that distributions of the trophic groups' biomass, yield, etc., around their mean trophic level follow a lognormal curve using the equation:

$$P_{ij} = \frac{1}{(TL_i - shift)\sigma_j \sqrt{2\pi}} exp \left[-\frac{\left(ln(TL_i - shift) - ln(\overline{TL_j} - shift) \right)^2}{2\sigma_j^2} \right] \qquad \text{(B.1)}$$

The lognormal distribution is defined by: a mean (the mean trophic level of the group, $\overline{TL_j}$), a standard deviation (σ_j denoted as sigmaLN in the R code) which is a measure of the trophic level variability within the group, and a *shift* parameter defining the theoretical trophic level characterised by a null variability in TL within group.

The create.smooth function enables the creation of this Smooth function using several input parameters. The parameter ecopath corresponds to the input data table (ecopath_guinee in the example). The parameter pas defining the splitting of trophic classes has by default a value of 0.1. The parameter smooth_type defines the form of the standard deviation (sigmaLN) wanted for the lognormal distribution. Three options are implemented:

1. If smooth_type=1 (choice by default), sigmaLN is constant. This constant sigmaLN is equal to the parameter sigmaLN_cst specified in the function, and has by default a value of 0.12. The shift parameter is set equal to 1.8 by default.

2. If smooth_type=2, this is equivalent to sigmaLN=smooth_param*ln(TL-0.05). The parameter smooth_param of this formula (also a parameter of the create.smooth function) defines the slope of the log-linear trophic level variability increase around the mean trophic level of the group. Based on our experience gained partially through observations, default parameters have been defined as follows: smooth_param=0.07 and shift=0.95. (No need to change the shift value in the function, let shift=NULL, it will be automatically set to 0.95 for smooth_type=2. Same thing for the parameter smooth_param).

3. If smooth_type=3, sigmaLN for each group is equal to the omnivory index calculated by Ecopath divided by the mean trophic level of the group. A warning message will appear if OIs are equal to 0, they will be automatically changed to a value of 0.01. The parameter shift is by default equal to 0. (No need to change the shift value in the function, let shift=NULL, it will be automatically set to 0 for smooth_type=3).

The create.smooth function returns a table of the distribution of each mean trophic level within trophic classes (i.e. how a given species or ecological group, characterized by a given and known mean trophic level, is distributed around this trophic level). This table will be used in the next step of the analysis for the construction of trophic spectra.

```
# default choice, constant sigmaLN

create.smooth(ecopath_guinee)

# sigmaLN=smooth_param*ln(TL-0.05)

create.smooth(ecopath_guinee, smooth_type=2)
```

A graphic function, plot(smooth), was developed in order to display this Smooth function. The input parameter is the table returned by the create.smooth function. It returns a plot with the lognormal curve for each present trophic class (Figure B.1).

```
plot(create.smooth(ecopath_guinee))
```
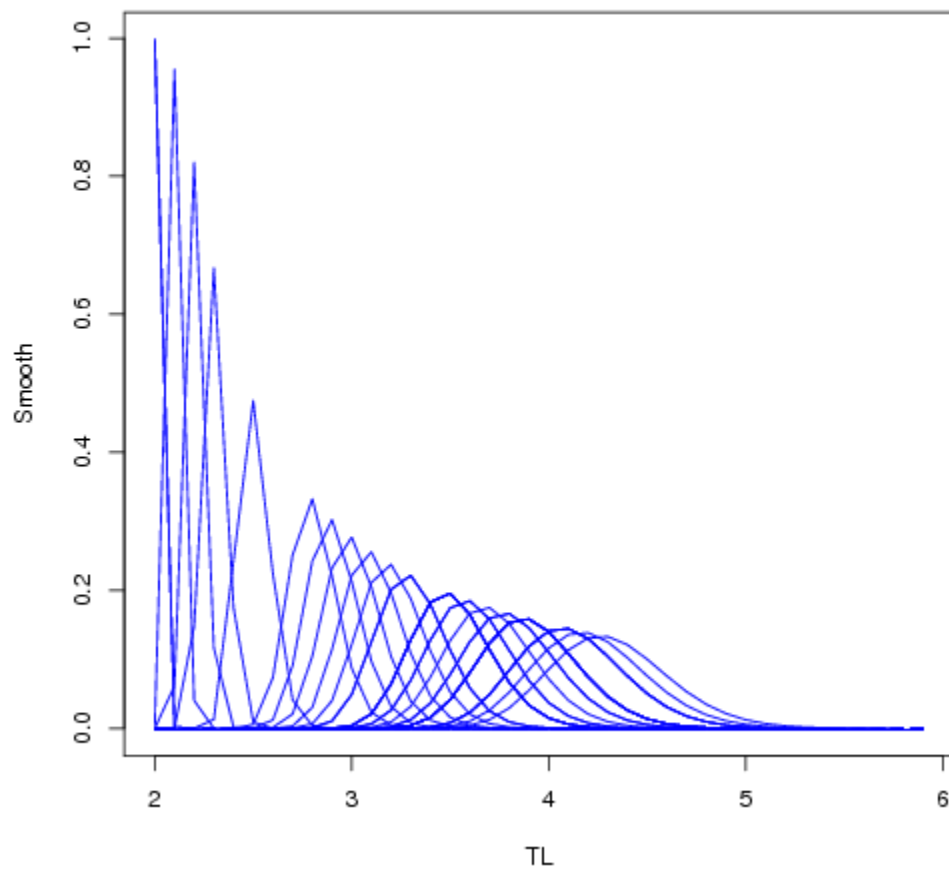

Figure B.1 Output of the plot(smooth) graphic function, applied to the Guinean ecosystem example. Each curve represents the distribution across trophic levels for all groups whose mean trophic level is equal to the mean value of the distribution. Only curves related to existing groups are displayed.

- Data transposition

The Transpose function enables the conversion of data referring to specific taxons or functional groups (Ecopath trophic groups for example) into data referring to trophic classes. This function uses the table returned by the create.smooth function. The concerned variables are the biomasses, or the catches or others... Using the Transpose function, these variables are distributed continuously along the trophic classes for each group. This function will be reused in the create.ETmain function to build a summary table with all the variables calculated by trophic class.

Transpose takes as input parameters the table returned by the create.smooth function (tab_smooth), the input data table (ecopath), and the name of the column the user wants to distribute by trophic class (column):

```
A ← create.smooth(ecopath_guinee)

# Transpose of the biomass column

T_biomass ← Transpose(A, ecopath_guinee, "biomass")

# Transpose of the catch.1 column

Transpose(A, ecopath_guinee, "catch.1")
```

Results can be displayed graphically using the plot(Transpose) function. It takes as input parameter the table returned by the Transpose function (tab_Trans). The user has the possibility to use a log scale for the y-axis (scale=log, the minimum value considered on the graph is conventionally set up at 1/10000 of the total biomass), and to enter a title (title). plot(tab_Trans, title=NULL, scale=NULL) returns the principal plots according to the selected column, in particular a plot by group and the associated trophic spectra (Figure B.2).

```
# title and log scale for the biomass

plot(T_biomass, title="biomass", log)
```
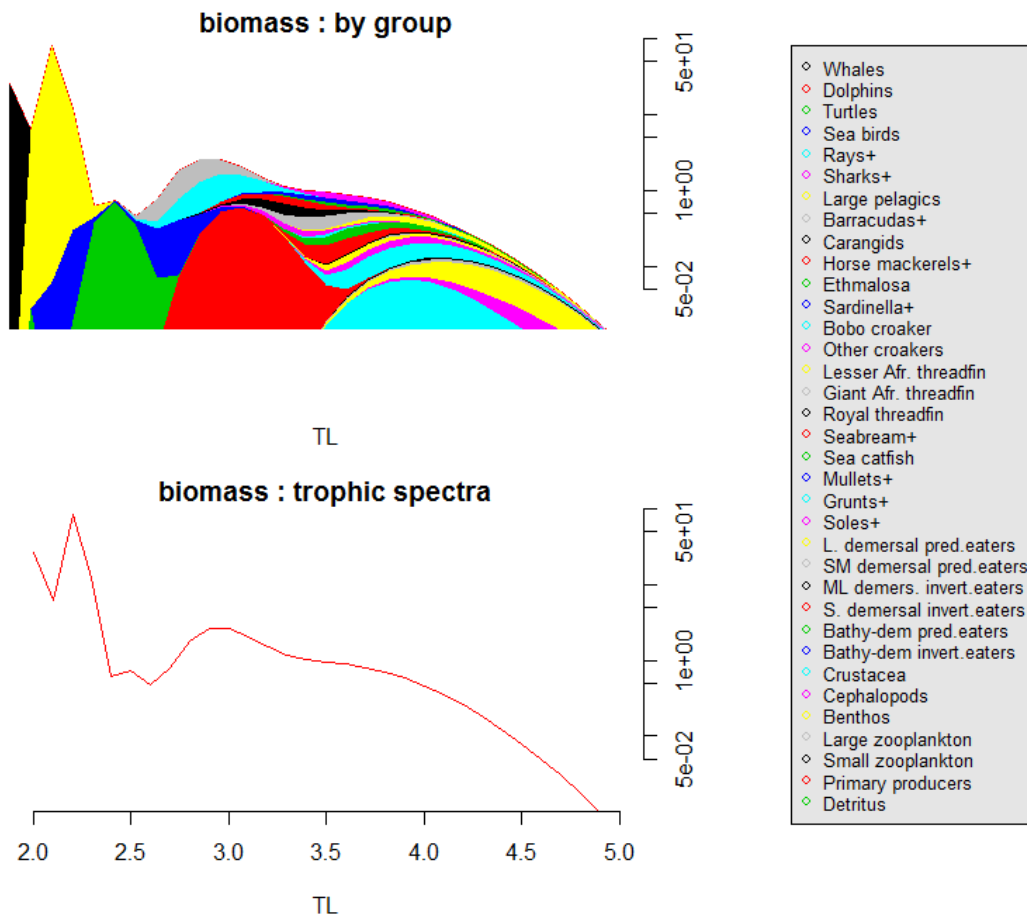

Figure B.2 Output of the plot(Transpose) graphical function applied to the biomass data per ecological group in the Guinean ecosystem (ecopath_guinee dataset). The top panel displays the distributions for each group, while the bottom panel displays the biomass trophic spectrum (BTS, i.e. the sum of all groups).

- ET_Main table creation

The create.ETmain function enables the creation of a summary table, ET_Main, containing the principal variables by trophic class. This function can be used directly, there is no

need of the previous steps Smooth and Transpose (however these steps are necessary to a good understanding of the EcoTroph model). It takes as input parameters the input data table (ecopath) and the parameters of the create.smooth function:

```
# constant sigmaLN

create.ETmain(ecopath_guinee)

# sigmaLN=smooth_param*ln(TL-0.05)

create.ETmain(ecopath_guinee, smooth_type=2)
```

In the ET_Main output table (Table B.2), some parameters directly come from the input table (biomass B, catch Y_tot), while some are calculated based on the definitions of EcoTroph parameters (e.g., fishing mortality Fish_mort=Y/B, fishing loss rate F_loss=Y/P, see details in Gascuel et al., 2009b).

```
# constant sigmaLN

ET_Main ← create.ETmain(ecopath_guinee)$ET_Main

ET_Main
```

The create.ETmain function also returns intermediate tables, i.e., the following tables are also contained in the returned list object: biomass, the table returned by the Transpose function for the column biomass; biomass_acc, the table biomass multiplied by the accessibility parameter; prod, the table corresponding to the production by trophic class; prod_acc, the table prod multiplied by the accessibility parameter; tab_smooth, the table returned by the create.smooth function; Y, the table(s) returned by the Transpose function for the column catch.(x).

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```
names(create.ETmain(ecopath_guinee))

[1] "ET_Main" "biomass" "biomass_acc" "prod" "prod_acc" "tab_smooth" "Y"
```

As previously, we developed a graphic function to display the main results: plot(ETmain). Different plots are created, e.g. the biomass trophic spectrum (BTS), the accessible biomass trophic spectrum (ABTS), the catch trophic spectrum (CTS). It takes as input parameter the list object returned by the create.ETmain function.

```
plot(create.ETmain(ecopath_guinee), log)
```

Naturally all the returned graphics are not exhaustive. The user can construct other ones using the returned list object. Moreover the plot(ETmain) function is implemented with a log scale parameter for the different trophic spectra. However, this does not always provide a good representation. We really encourage users to test different scales for the y-axis. Some plots could be falsely interpreted with no awareness of the y-axis form importance.

Table B.2 create.ETmain(ecopath_guinee)$ET_Main results (extracts).

TL	B	B_acc	P	P_acc	Kin	Kin_acc	Y_tot	F_loss	N_loss	Fish_mort
1	359.00	0.00	5796.00	0.00	16.14	1.00	0.00	0.00	1.73	0.00
2	25.73	0.00	1029.20	0.00	40.00	0.68	0.00	0.00	43.41	0.00
2.1	6.26	0.00	13.40	0.00	2.14	0.68	0.00	0.00	-24.00	0.00
2.2	82.06	0.06	147.64	0.04	1.80	0.68	0.01	0.00	19.42	0.00
2.3	11.94	0.27	21.17	0.20	1.77	0.74	0.05	0.00	31.57	0.00
2.4	0.62	0.44	0.90	0.57	1.44	1.31	0.24	0.00	-1.89	0.38
…	…	…	…	…	…	…	…	…	…	…

B.5   ET-Diagnosis simulation tool

ET-Diagnosis is used to simulate the effect of different fishery mortality scenarios on trophic spectra coming from ET-Transpose (see above). Thus different effort multipliers

(Mul_eff variable), ranging conventionally from 0 to 5, are applied to the initial fishing mortalities F_τ. Mul_eff=0 corresponds to a fishery closure (F=0), and allows users to rebuilt an estimate of the unexploited status of the studied ecosystem. Flow equations enable the calculation of the biomasses B_τ, the productions P_τ and the catches Y_τ at the equilibrium for each trophic class and Mul_eff. The other variables contained in the ET_Main table are also treated. All the trophic spectra representing the situation at equilibrium are so obtained for each Mul_eff. Effects of fishery mortality changes at an ecosystem scale include biomass, accessible biomass, and kinetic changes, but also impacts on the mean trophic levels of the catch and of the total biomass. The model provides an overview of the current fishing impact on the ecosystem (compared to the unexploited state), and some long term forecasts on the consequences of increasing or decreasing fishing pressures. This model also enables to see how different ecosystem functioning hypotheses (values of the extent recycling, top-down effect) could affect the ecosystem and trophic scale properties.

ET-Diagnosis is implemented through the create.ETdiagnosis function. It takes as input parameters the list object returned by the create.ETmain function, Mul_eff a vector of the different effort multipliers, and the specific parameters of the ET-diagnosis simulations:

- Beta, a parameter taking values between 0 and 1, which defines the intensity of the biomass recycling by the microbial loop (default value set to 0.1);

- TopD, a parameter taking values between 0 and 1, which defines the intensity of the top-down control of predators on their prey (default value set to 0.4);

- FormD, a parameter taking values between 0 and 1, which defines the functional relationship between preys and predators (default value set to 0.5).

This function returns two types of results for each simulated effort multiplier: indices calculated at the ecosystem scale for each effort multiplier, and the catches, biomasses, accessible biomasses, productions... for each trophic class.

```
ETmain ← create.ETmain(ecopath_guinee)

create.ETdiagnosis(ETmain)

# change of the top-down parameter

create.ETdiagnosis(ETmain, TopD=0.6)
```

A graphic function, plot(m,scale=null,maxrange=null), displays the principal plots coming from the function create.ETdiagnosis: the biomass, predator biomass, catches ratio plots for the different effort multipliers, and the principle trophic spectra. This function takes as input parameters the list object returned by the create.ETdiagnosis function (m), one scale parameter for the y-axis of the BTS (scale, log or not), and the maximum wanted for the x-axis (maxrange). Naturally all the returned graphics are not exhaustive as users can construct other ones using the returned list object. As previously mentioned, users are really encouraged to test different scales for the y-axis. Figure B.3 is one major graphic of the eight displayed by the function.

```
# log scale for the BTS

diag ← create.ETdiagnosis(ETmain)

plot(diag, log)
```

B.6   Conclusion

This appendix describes the principle functions of the EcoTroph package. The package enables the analysis of fishing impacts on aquatic trophic networks in a simple way, and also the

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simulation of various fisheries in terms of catch. New simulation tools have been developed to improve the model and enable the implementation of more options regarding the fisheries scenarios. The package is available on the Comprehensive R Archive Network (CRAN, http://CRAN.R-project.org/) and users are encouraged to provide feedback in order to enhance the tool. All the information contained in this appendix is not exhaustive. More details are available in the package help, and on the website (http://sirs.agrocampus-ouest.fr/EcoTroph). Feel free to contact the authors for any problem encountered while using the package.
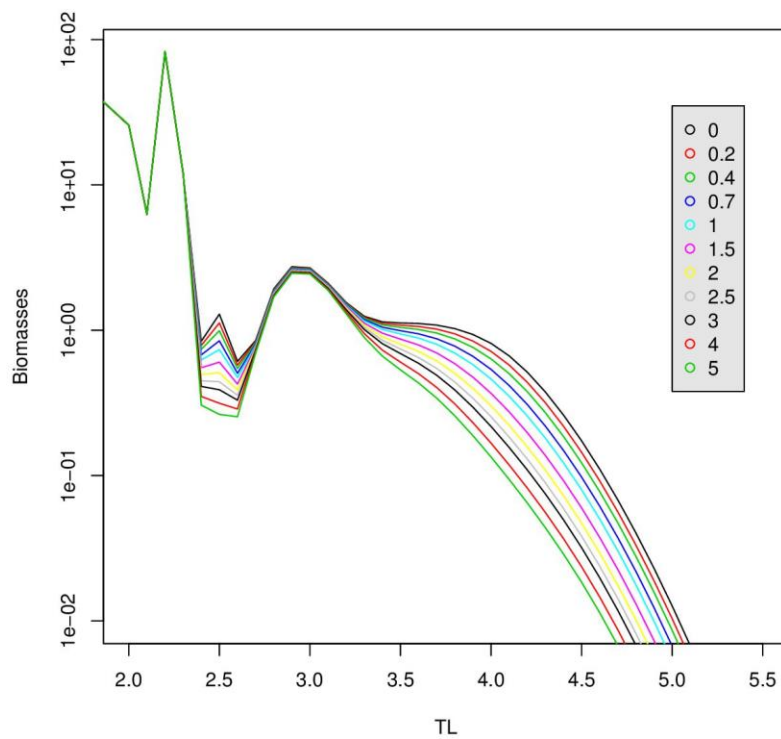
Figure B.3 Simulated biomass trophic spectra (BTS) of the Guinean ecosystem for various fishing effort multipliers ranging from 0 (no fishing) to 5. Such a graph highlights the fishing effects on trophic levels around 2.5 or higher than 3.4, with larger impact for the top predators (highest TLs). In contrast, the low and intermediate ones are less damaged.

Appendix C Details on the Goodyear compensation ratio

A consumption limitation modifier H was integrated in Eq. (3.7), which modifies $\Phi_{\tau+\Delta\tau}$ using an asymptotic effect scaled relative to the reference biomass flow at trophic level $\tau+\Delta\tau$, $\Phi_{\text{ref},\tau+\Delta\tau}$ (reference situation before simulation; see Figure 3.4). H, the consumption limitation modifier (Eq. (3.19)), is of the same form as the foraging arena equation (Eq. (3.17)). It assumes that a proportion ω of the biomass flow is due to ontogenetic changes in feeding, and the remaining proportion is dependent on the relative biomass flow rate $\Phi_{\tau+\Delta\tau}/\Phi_{ref,\tau+\Delta\tau}$ and the Goodyear compensation ratio G. G is a parameter coming from the analysis of recruits vs. spawning stock biomass (see Walters et al., 2008), and it is a good proxy for the biomass compensation ratio, i.e., the maximum possible relative increase in Q/B_{pred} when B_{pred} is greatly reduced (Ahrens et al., 2012; Walters et al., 1997).

In fact, the Goodyear (1977) compensation ratio is originally defined using the plot of recruits vs spawning stock biomass. The compensation ratio is the ratio of the slope of the plot near zero spawning stock biomass (maximum recruits per spawner biomass) to the recruits/spawner biomass at the unfished equilibrium. It measures how much juvenile survival rate increases from the unfished to nearly extinct spawner biomass. To get this plot for a multi-stanza species in an Ecosim model, you have to fish the stock down to a low level, and then let it recover to the unfished level. As a consequence, there is no simple way to calculate this without doing Ecosim runs specifically set up to expose the stock-recruit relationship. In fact, there is no explicit recruitment-numbers accounting in ecosystem dynamics models. The quantity corresponding to the compensation ratio is the population 'r' value, the maximum surplus production per biomass at low biomass (with surplus production equal to zero at unfished equilibrium) (Walters and Martell, 2004). In Ecosim, surplus production is defined as: $(g \times$

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$Q) - (M \times B_{pred})$, with $M = M_2 + M_0$ (non fishing mortality rate, see Figure 3.2), and $P = g \times Q$ (production is a proportion of consumption with 'g' the food conversion efficiency). Thus, surplus production per biomass is defined as: $g \times Q/B_{pred} - M$. Q basically varies as defined in Eq. (3.17), so Q/B_{pred} approaches $a \times B_{prey}/2$ as B_{pred} approaches zero. This means that 'r' is given approximately by: $g \times a \times B_{prey}/2 - M$, assuming B_{prey} does not increase much as B_{pred} decreases (the most common situation).

The predator search rate 'a' is given by Eq. (C.1):

$$a = 2 \times k \times \left(Q^0/B^0_{prey}\right)/[B^0 \times (k - 1)] \tag{C.1}$$

where 'k' is the input vulnerability ratio of maximum prey mortality rate (Q/B_{prey}) to Ecopath base prey mortality rate Q^0/B^0_{prey}. Thus, 'r' depends negatively on 'k': as 'k' approaches 1, 'a' approaches infinity, and so does 'r'. As 'k' increases toward infinity, 'r' decreases substantially. The bottom line is that, in biomass dynamics using the foraging arena equation, 1/k is a good proxy for the biomass 'compensation ratio' G. The most common vulnerability exchange multiplier values that come from fitting time series data are in the range 1.1-10, roughly implying G values between 20 and about 2 respectively. More precisely, G should be approximately equal to 2k/(k-1).
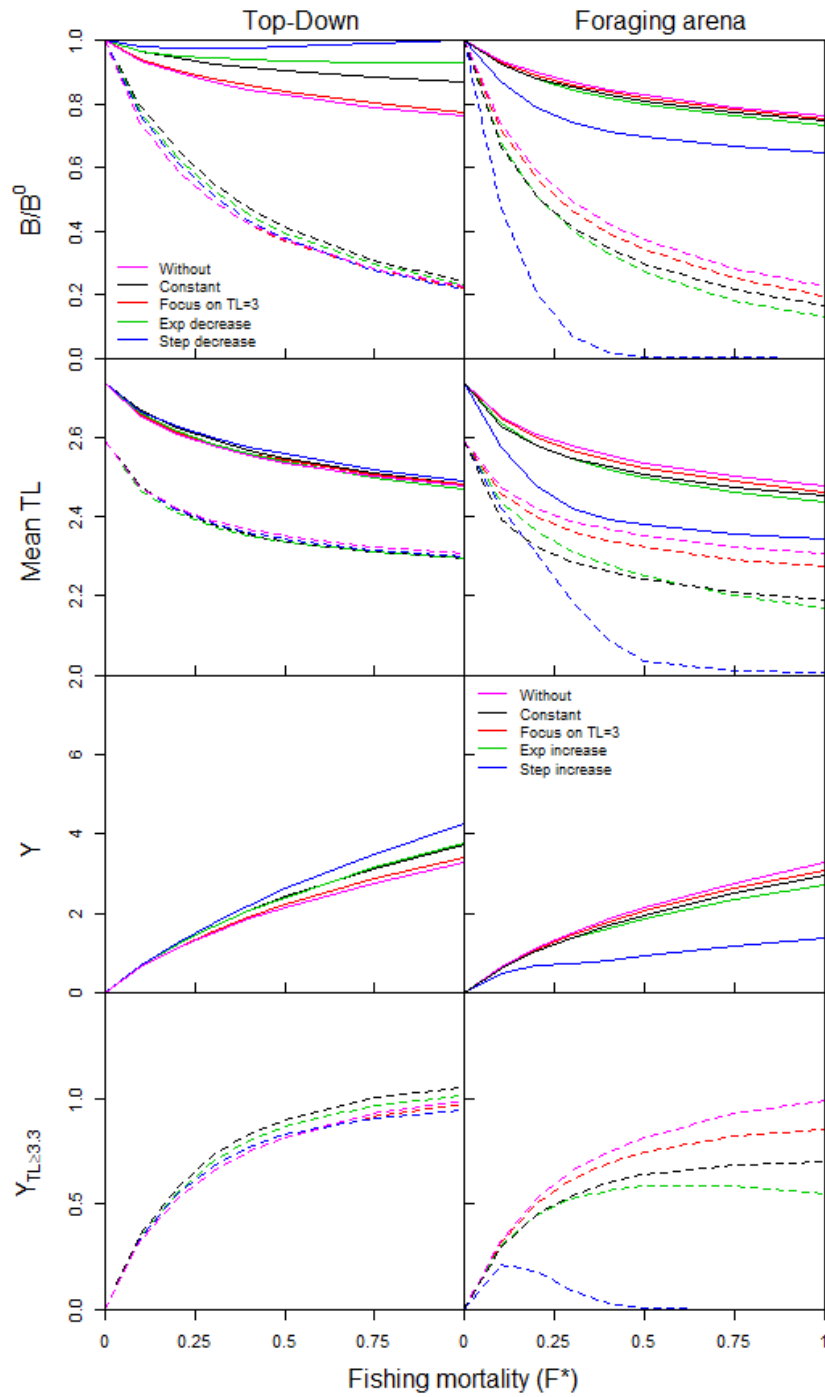
Figure D.1 Value of EcoTroph outputs function of the fishing mortality (F*) used in simulation: the relative

biomass and predator biomass ratios (B/B^0 and $B_{TL\geq3.3}/B^0_{TL\geq3.3}$, dashed lines for predator variables), the mean

trophic level of the biomass and predator biomass, the total catch (Y), and the predator catch ($Y_{TL \geq 3.3}$). The left and right columns refer respectively to the different EcoTroph simulations with varying top-down and foraging arena control scenarios. The different TL-dependent effects are represented using black for scenarios where controls are constant over TLs, red where controls focus on TL=3, green where controls exponentially increase over TLs, and blue where controls step increase with strong controls for high TLs only. The simulated exploited ecosystem without foraging arena and top-down controls (purple line) was also represented.

Appendix E Supplementary tables to Chapter 4

Table E.1 Basic inputs and estimated outputs (bold) of the Bonifacio MPA Ecopath model (TL: trophic level; B: biomass; P/B: production/biomass ratio; Q/B: consumption/biomass ratio; EE: ecotrophic efficiency; P/Q: production/consumption ratio; Acc.: accessibility to fisheries; U/Q: unassimilated consumption; Y: catches).

Group name	TL	B (t.km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	EE	P/Q	Acc.	U/Q	Y (t.km^{-2}.year^{-1})
Tursiops truncatus	**5.20**	0.01	0.01	13.49	**0.00**	**0.00**	0.0	0.11	0
Sphyraena sphyraena	**4.93**	0.25	0.60	5.00	**0.02**	**0.12**	0.9	0.11	0.003
Scyliorhinus canicula	**4.60**	0.04	1.32	4.06	**0.01**	**0.33**	0.9	0.11	0.001
Pisivorous fish	**4.21**	3.55	0.70	3.80	**0.42**	**0.18**	0.9	0.11	0.047
Small pelagic feeders	**4.55**	1.15	0.93	4.47	**0.42**	**0.21**	0.7	0.11	0.021
Epinephelus XL	**4.48**	0.09	0.16	1.32	**0.07**	**0.12**	0.8	0.11	0.001
Epinephelus L	**4.23**	0.53	0.53	2.87	**0.48**	**0.18**	0.0	0.11	0
Epinephelus S	**4.01**	0.25	1.80	8.01	**0.59**	**0.22**	0.0	0.11	0
Opportunist piscivorous fish	**4.09**	7.59	0.63	4.79	**0.94**	**0.13**	0.8	0.11	0.041
Cephalopods	**3.91**	3.42	2.12	5.27	**0.98**	**0.40**	0.8	0.11	0.004
Birds	**3.63**	0.00	5.74	85.03	**0.03**	**0.07**	0.0	0.11	0
Benthic invertebrate feeders	**3.57**	1.95	0.63	4.65	**0.98**	**0.14**	0.9	0.2	0.024
Zooplanktivorous fish	**3.22**	13.30	0.45	9.29	**0.97**	**0.05**	0.5	0.2	0.000
Mollusc feeders	**3.18**	10.84	0.72	6.49	**0.96**	**0.11**	0.6	0.2	0.010
Benthic invertebrate feeders 2	**3.35**	11.21	0.77	6.19	**0.96**	**0.12**	0.5	0.2	0.009
Shrimps	**2.90**	**7.87**	3.08	7.20	0.80	**0.43**	0.0	0.2	0
Macroplanktivorous fish	**3.34**	1.03	0.70	5.39	**0.79**	**0.13**	0.8	0.2	0.012
Decapods	**2.90**	29.28	3.11	15.39	**0.93**	**0.20**	0.0	0.2	0
Superior crustacea	**2.82**	2.43	0.45	7.50	**0.52**	**0.06**	**0.0**	0.2	0.020
Gastropods	**2.43**	**104.25**	1.94	10.89	0.80	**0.18**	0.0	0.38	0
Zooplankton	**2.43**	**3.90**	50.86	172.92	0.80	**0.29**	0.0	0.13	0
Polychaetes	**2.46**	49.87	3.42	19.57	**0.98**	**0.17**	0.0	0.58	0
Suspensivors	**2.26**	**247.48**	1.52	6.78	0.80	**0.22**	0.0	0.6	0

Group name	TL	B (t.km⁻²)	P/B (year⁻¹)	Q/B (year⁻¹)	EE	P/Q	Acc.	U/Q	Y (t.km⁻².year⁻¹)
Echinoderms	**2.12**	11.20	0.51	2.82	**0.99**	**0.18**	0.0	0.4	0
Protozoa plankton	**2.06**	**6.99**	90.00	305.16	0.80	**0.29**	0.0	0.4	0
Sarpa salpa L	**2.17**	0.10	1.33	24.12	**0.58**	**0.06**	0.0	0.8	0
Sarpa salpa S	**2.49**	0.20	1.36	49.64	**0.89**	**0.03**	0.0	0.55	0
Other crustacean	**2.04**	10.02	20.54	94.00	**0.25**	**0.22**	0.0	0.75	0
Amphipods	**2.09**	**27.88**	9.15	22.09	0.80	**0.41**	0.0	0.55	0
Bivalves	**2.00**	**35.97**	2.10	8.95	0.80	**0.23**	0.0	0.4	0
Macroplankton	**2.03**	**62.37**	25.43	71.20	0.80	**0.36**	0.0	0.4	0
Phytoplankton	**1.00**	**17.43**	114.00	-	0.60	-	0.0	0	0
Macro-algae	**1.00**	**647.71**	5.00	-	0.55	-	0.0	0	0
Posidonia oceanica	**1.00**	500.00	1.00	-	**0.03**	-	0.0	0	0
Detritus	**1.00**	1.00	-	-	**0.45**	-	0.0	0	0

Table E.2 Basic inputs and estimated outputs (bold) of the Port-Cros MPA Ecopath model (TL: trophic level; B: biomass; P/B: production/biomass ratio; Q/B: consumption/biomass ratio; EE: ecotrophic efficiency; P/Q: production/consumption ratio; Acc.: accessibility to fisheries; U/Q: unassimilated consumption; Y: catches). Fish groups were named using the most abundant species of the group. a '+' indicating the presence of secondary species.

Group name	TL	B (t.km⁻²)	P/B (year⁻¹)	Q/B (year⁻¹)	EE	P/Q	Acc.	U/Q	Y (t.km⁻².year⁻¹)
Seabirds	**4.17**	0.29	0.40	73.20	**0.00**	**0.01**	0.0	0.11	0
Rays	**4.39**	**0.03**	0.20	1.99	0.40	**0.10**	1.0	0.2	0.003
Amberjack and dentex +	**4.11**	5.55	0.24	2.44	**0.11**	**0.10**	0.6	0.11	0.029
Large-scaled scorpionfish +	**4.24**	0.49	0.52	4.48	**0.67**	**0.12**	1.0	0.11	0.079
Scorpionfishes and combers +	**3.82**	4.29	0.60	3.99	**0.29**	**0.15**	0.8	0.11	0.031
Dusky grouper - large	**4.40**	4.32	0.10	0.67	**0.00**	**0.15**	0.0	0.11	0
Dusky grouper - medium	**4.27**	0.43	0.44	1.56	**0.72**	**0.28**	1.0	0.11	0.000
Dusky grouper - small	**4.00**	0.25	1.53	4.40	**0.40**	**0.35**	1.0	0.11	0.000
Cephalopods	**3.63**	3.00	2.34	7.80	**0.95**	**0.30**	0.8	0.11	0.017
Stripped red mulet +	**3.67**	0.24	0.84	5.65	**0.96**	**0.15**	0.1	0.2	0.030
Pagellus	**3.67**	**0.67**	0.42	4.15	0.95	**0.10**	1.0	0.2	0.003

Group name	TL	B (t.km⁻²)	P/B (year⁻¹)	Q/B (year⁻¹)	EE	P/Q	Acc.	U/Q	Y (t.km⁻².year⁻¹)
Blennies +	**3.33**	0.15	0.59	5.94	**0.98**	**0.10**	0.0	0.2	0
Pipefishes +	**3.44**	0.02	1.38	9.92	**0.83**	**0.14**	0.0	0.2	0
Gobies	**3.37**	0.43	1.12	5.60	**0.78**	**0.20**	0.0	0.2	0
Horse mackerels & sand smelts +	**3.58**	20.00	0.56	5.56	**0.92**	**0.10**	0.1	0.2	0.012
Diplodus +	**3.08**	3.63	0.50	5.03	**0.66**	**0.10**	0.8	0.2	0.029
Wrasses	**2.97**	5.04	0.53	5.27	**0.95**	**0.10**	0.8	0.2	0.019
Crabs	**2.64**	3.61	1.61	14.00	**0.76**	**0.12**	**0.0**	0.2	0.019
Decapods	**2.69**	**14.30**	2.30	23.00	0.90	**0.10**	**0.0**	0.2	0.012
Sea stars	**2.72**	0.70	0.25	1.67	**0.18**	**0.15**	0.0	0.4	0
Large zooplankton	**3.13**	**2.83**	25.00	125.00	0.80	**0.20**	0.0	0.13	0
Bivalves	**2.10**	2.79	2.46	15.87	**0.94**	**0.16**	0.0	0.4	0
Gastropods	**2.24**	**20.92**	1.91	10.71	0.80	**0.18**	0.0	0.38	0
Suspensivores	**2.29**	**34.13**	1.70	14.01	0.80	**0.12**	0.0	0.6	0
Brittle stars +	**2.05**	**0.79**	0.49	3.24	0.80	**0.15**	0.0	0.4	0
Sea worms	**2.34**	**36.49**	1.82	11.53	0.80	**0.16**	0.0	0.58	0
Mullets	**2.29**	4.50	0.45	4.53	**0.59**	**0.10**	0.0	0.55	0
Gorgonians	**2.24**	40.56	0.08	0.53	**0.00**	**0.15**	0.0	0.6	0
Small crustaceans	**2.15**	31.05	4.00	33.40	**0.91**	**0.12**	0.0	0.2	0
Small zooplankton	**2.20**	**14.29**	50.00	170.00	0.80	**0.29**	0.0	0.4	0
Sea urchins	**2.16**	38.20	0.19	1.27	**0.66**	**0.15**	0.0	0.5	0
Amphipods	**2.25**	**32.29**	4.00	20.00	0.80	**0.20**	0.0	0.27	0
Sea cucumbers	**2.05**	76.26	0.25	1.67	**0.25**	**0.15**	0.0	0.7	0
Salema - adults	**2.00**	5.40	0.25	2.54	**0.13**	**0.10**	1.0	0.8	0.022
Salema - juveniles	**2.00**	4.10	0.81	5.24	**0.42**	**0.16**	1.0	0.55	0.017
Foraminifera	**2.00**	**18.35**	50.00	166.67	0.80	**0.30**	0.0	0.2	0
Posidonia	**1.00**	2038.00	2.00	0.00	**0.18**	-	0.0	0	0
Shallow seaweeds	**1.00**	140.96	4.43	0.00	**0.75**	-	0.0	0	0
Deep seaweeds	**1.00**	40.95	1.57	0.00	**0.67**	-	0.0	0	0
Phytoplankton	**1.00**	**32.84**	112.65	0.00	0.60	-	0.0	0	
Detritus	**1.00**	1.00	0.00	-	**0.51**	-	0.0	0	

Table E.3 Basic inputs and estimated outputs (bold) of the Bamboung MPA Ecopath model (TL: trophic level; B: biomass; P/B: production/biomass ratio; Q/B: consumption/biomass ratio; EE: ecotrophic efficiency; P/Q: production/consumption ratio; Acc.: accessibility to fisheries; U/Q: unassimilated consumption; Y: catches)

Group name	TL	B (t.km⁻²)	P/B (year⁻¹)	Q/B (year⁻¹)	EE	P/Q	Acc.	U/Q	Y (t.km⁻².year⁻¹)
Sharks	**4.28**	0.00	0.13	4.99	**0.00**	**0.03**	0.5	0.11	0
Dolphins	**3.94**	0.00	0.07	12.12	**0.00**	**0.01**	0.0	0.11	0
Birds	**3.48**	0.00	0.50	79.50	**0.00**	**0.01**	0.0	0.11	0
Rays	**3.23**	0.09	0.40	3.39	**0.64**	**0.12**	0.6	0.2	0
Croakers	**3.59**	0.38	0.35	7.17	**0.84**	**0.05**	0.9	0.11	0
Barracudas	**3.85**	0.22	0.33	6.18	**0.38**	**0.05**	0.9	0.11	0
Giant Threadfin	**3.66**	0.20	0.30	6.54	**0.69**	**0.05**	0.9	0.11	0
Snappers	**3.30**	0.41	0.43	9.89	**0.71**	**0.04**	0.9	0.11	0
Puffer	**3.31**	0.26	0.31	6.13	**0.94**	**0.05**	0.9	0.11	0
Biglip grunt	**3.15**	0.13	0.61	10.63	**0.74**	**0.06**	0.8	0.11	0
Pompano	**3.30**	0.63	0.39	6.41	**0.76**	**0.06**	0.9	0.2	0
Jacks	**3.38**	0.11	0.72	17.49	**0.77**	**0.04**	0.3	0.2	0
Sea catfishes	**3.38**	1.34	0.43	9.74	**0.72**	**0.04**	0.9	0.2	0
Ladyfish	**3.47**	0.16	0.39	10.29	**0.91**	**0.04**	0.9	0.11	0
African moony	**3.16**	0.09	0.99	18.27	**0.77**	**0.05**	0.9	0.2	0
Tonguesole	**3.25**	0.02	0.38	6.51	**0.75**	**0.06**	0.8	0.2	0
Sardinella	**2.75**	0.28	1.10	18.12	**0.58**	**0.06**	0.7	0.55	0
Mojarra	**3.03**	0.27	1.05	13.64	**0.56**	**0.08**	0.9	0.2	0
Bonga	**2.57**	0.35	0.93	28.98	**0.58**	**0.03**	0.9	0.55	0
Mullets	**2.67**	0.60	0.73	28.48	**0.63**	**0.03**	0.9	0.55	0
Grunts	**3.18**	0.29	0.58	9.71	**0.68**	**0.06**	0.9	0.11	0
Tilapias	**2.03**	0.16	0.93	33.93	**0.52**	**0.03**	0.9	0.55	0
Small Benthosfeeders	**2.35**	**0.40**	3.46	19.89	0.79	**0.17**	0.0	0.2	0
Shrimps	**2.53**	**2.79**	5.20	22.00	0.80	**0.24**	0.0	0.2	0
Crabs	**2.74**	**3.86**	2.58	8.50	0.79	**0.30**	0.0	0.2	0
Macrobenthos	**2.00**	**51.54**	1.13	10.00	0.49	**0.11**	0.0	0.5	0
Meiobenthos	**2.12**	**7.35**	3.94	50.00	0.81	**0.08**	0.0	0.5	0
Zooplankton	**2.05**	**3.38**	49.85	150.00	0.64	**0.33**	0.0	0.4	0
Phytoplankton	**1.00**	**9.17**	138.00	0.00	0.60	-	0.0	0	0

Group name	TL	B (t.km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	EE	P/Q	Acc.	U/Q	Y (t.km^{-2}.year^{-1})
Microphytobenthos	**1.00**	**22.27**	15.00	0.00	0.50	-	0.0	0	0
Detritus	**1.00**	1.00	-	-	**0.32**	-	0.0	0	0

Appendix F Supplementary tables and figures to Chapter 5

Table F.1 Details on the 127 Ecopath models used in this meta-analysis (extracted from EcoBase): the model number, name, and location, the number of Ecopath groups, the minimum, maximum, and mean depths (as indicated in the supporting references), the average sea surface temperature (SST), the ecosystem type, the latitude class, and the associated references (detailed references are given below the table and at http://sirs.agrocampus-ouest.fr/EcoBase/, using the corresponding references number). More details are available for each model on the EcoBase website using the discovery tool and the model name (http://sirs.agrocampus-ouest.fr/EcoBase/).

Number	Name	Location	Min depth	Max depth	Mean depth	SST	Ecosystem type	Latitude	Ref
2	Prince William Sound old model	Prince William Sound	0	800	300	8.25	shelf_slope	58-90	3
7	Azores archipelago	Azores archipelago	0	3000		19.12	shelf_slope	30-58	8
28	Central Atlantic 50s	Atlantic Ocean, central				26.22	ocean	0-30	27
29	Central Atlantic 90s	Atlantic Ocean, central				26.22	ocean	0-30	27
40	Eastern Scotian Shelf 80s	Nova-Scotia, Eastern	0	200		8.49	shelf_slope	30-58	34, 35
41	Eastern Scotian Shelf 90s	Nova-Scotia, Eastern	0	200		8.49	shelf_slope	30-58	34, 35
48	Galapagos	Floreana Island	0	20		23.53	reef	0-30	43
49	Gambia 1986	Gambia, continental shelf	0	200		25.09	shelf_slope	0-30	44
51	Gambia 1995	Gambia, continental shelf	0	200		25.09	shelf_slope	0-30	45
53	Golfo Dulce	Gulf Dulce	0	215		28.65	bay	0-30	47
57	Guinee-Bissau	Guinea-Bissau, continental shelf	0	200		26.16	shelf_slope	0-30	51
58	Gulf of Mexico	Gulf of Mexico				26.10	shelf_slope	0-30	52
63	Barents Sea 1990	Barents Sea				0.29	shelf_slope	58-90	57
64	Barents Sea 1995	Barents Sea				0.29	shelf_slope	58-90	57
68	Icelandic shelf	Iceland, shelf				5.76	shelf_slope	58-90	62

Number	Name	Location	Min depth	Max depth	Mean depth	SST	Ecosystem type	Latitude	Ref
93	Mandinga lagoon	Veracruz, Mandinga lagoon	0	3		26.32	lagoon	0-30	82
99	Mid Atlantic Bight	Atlantic Bight, middle	0	200		14.57	shelf_slope	30-58	87
105	Newfoundland Grand Banks 1900	Newfoundland	0	1000		7.46	shelf_slope	30-58	95
107	Newfoundland Grand Banks 1980	Newfoundland	0	1000		7.46	shelf_slope	30-58	91, 94
108	Newfoundland Grand Banks 1990	Newfoundland	0	1000		7.46	shelf_slope	30-58	91, 94
112	North Atlantic 90s	Atlantic Ocean, central				18.68	ocean	30-58	27
115	Northern Benguela 1956	Benguela, Northern	0	500		18.41	upwelling	0-30	100, 101
116	Northern Gulf St Lawrence 1980	Gulf of St Lawrence, Northern	37	500		4.42	shelf_slope	30-58	103, 365, 366
118	Northwest Africa	Africa, Northwestern				22.72	shelf_slope	0-30	105
130	San Pedro Bay	San Pedro Bay, Leyte Gulf	0	36.6	20	28.63	bay	0-30	113
135	Sierra Leone 1964	Sierra Leone, shelf and slope waters off	0	200		27.89	shelf_slope	0-30	119
136	Sierra Leone 1978	Sierra Leone, shelf and slope waters off	0	200		27.89	shelf_slope	0-30	119
137	Sierra Leone 1990	Sierra Leone, shelf and slope waters off	0	200		27.89	shelf_slope	0-30	119
153	Tampa Bay	Gulf of Mexico				24.82	bay	0-30	131
172	West Coast Vancouver Island	Vancouver Island, Western	0	200		11.38	shelf_slope	30-58	527
173	West Florida Shelf	Florida shelf, Western	0	200		25.12	shelf_slope	0-30	148, 528
175	Western Bering Sea	Bering Sea, Western	0	200		3.07	shelf_slope	58-90	150
179	Bamboung 2003	Sine Saloum estuary, Bolong de Bamboung	0	15		25.17	lagoon	0-30	155
180	Bamboung 2006-08	Sine Saloum estuary, Bolong de Bamboung	0	15		25.17	lagoon	0-30	155
183	Eastern Bering Sea 1980	Bering Sea, Eastern	0	500		3.99	shelf_slope	30-58	15
227	Iceland 1950	Iceland, shelf				5.65	shelf_slope	58-90	59
239	Central Gulf of California	Gulf of California, Central	5	65		24.08	coastal	0-30	29, 30
240	Sonda de Campeche	Gulf of Mexico, Sonda de	20	200		26.85	shelf_slope	0-30	120

Number	Name	Location	Min depth	Max depth	Mean depth	SST	Ecosystem type	Latitude	Ref
		Campeche							
241	Huizache-Caimanero	Huizache-Caimanero lagoon				26.57	lagoon	0-30	58
242	Alto Golfo de California	Gulf of California, North, Alto Golfo de California			200	22.17	shelf_slope	30-58	6
247	Celestun mangrove	Celestun lagoon	0	3		26.74	lagoon	0-30	25, 524
252	Aleutian Islands 1963	Aleutian Islands	0	500		5.74	shelf_slope	30-58	4, 5
266	Kuosheng Bay	Kuosheng Bay	0		15	23.92	bay	0-30	64
269	Looe Key National Marine Sanctuary	Looe Key				26.66	reef	0-30	80, 175
279	Prince William Sound Ecosystem	Prince William Sound	0	800	300	8.25	shelf_slope	58-90	1, 2, 174
282	Venezuela shelf	Venezuela shelf	0	200		27.10	shelf_slope	0-30	144
290	Bahia Ascencion	Bahia La Ascencion			2.5	27.66	bay	0-30	9
305	West Coast of Sabah	Sabah, Western	10	60		28.77	coastal	0-30	147
307	Jalisco and Colima Coast	Jalisco and Colima	0	90		27.54	coastal	0-30	63
324	Virgin Islands	Virgin Islands, British				27.42	reef	0-30	139
325	Southern of Gulf California	Gulf of California, Southern	20	140		26.38	shelf_slope	0-30	166
328	Strait of Georgia	Strait of Georgia				10.66	shelf_slope	30-58	128
400	Ainsworth_1990_RajaAmpat	Raja Ampat				28.96	reef	0-30	300, 301
401	Ainsworth_2005_RajaAmpat	Raja Ampat				28.96	reef	0-30	300, 301, 509
402	Albouy_2000_BSNR_Corsica	Corsica, Bonifacio Strait Natural Reserve		158		18.24	coastal	30-58	304
403	Araujo_1994_WEnglishChannel	English Channel, Western	0	100		12.72	shelf_slope	30-58	151, 152, 428
405	Bulman_1986_NWS_Australia	Australian Shelf, North West	20	200		26.91	shelf_slope	0-30	308
406	Bulman_1994_EBassStrait	East Bass Strait	25	700		16.87	shelf_slope	30-58	310
410	Cheung_1970_NSouthChinaSea	China Sea, North South	0	200		25.28	shelf_slope	0-30	314
412	Christensen_1963_GulfThailand	Gulf of Thailand	10	50		28.98	coastal	0-30	56
413	Christensen_1974_NorthSea	North Sea				10.04	shelf_slope	30-58	317

Number	Name	Location	Min depth	Max depth	Mean depth	SST	Ecosystem type	Latitude	Ref
414	Christensen_1970_WMalaysia	Malaysia Peninsula, Western				29.28	shelf_slope	0-30	146, 318
415	Christensen_1994_SWVietnam	Viet Nam coast, Southwest				27.84	coastal	0-30	318
417	CisnerosMontemayor 1972_BajaCaliforniaSur	Baja California Sur				21.50	shelf_slope	0-30	320, 441
419	Coll_1990_NCAdriaticSea	Adriatic Sea, Northern and Central	10	273	75	17.74	shelf_slope	30-58	322
420	Coll_1978_SCatalanSea	Mediterranean Sea, Northwestern, Catalan Sea, Southern	50	400		18.77	shelf_slope	30-58	323
421	Coll_1975_NCAdriaticSea	Adriatic Sea, Northern and Central	10	273	75	17.74	shelf_slope	30-58	324, 453
429	FalkPetersen_1993_Norway	Troms County, Sørfjord		130		7.01	bay	58-90	333
431	Fulton_1994_PortPhillipBay	Port Phillip Bay	0	24		15.50	bay	30-58	337, 520
432	Fulton_2007_Ningaloo	Ningaloo				25.18	reef	0-30	176, 177
438	Guenette_1963_SEAlaska	Alaska, Southeast		1000		9.00	shelf_slope	30-58	4
439	Guenette_1953_Peru	Peruvian coast				20.96	upwelling	0-30	343
441	Haputhantri_2000_SriLanka	Sri Lanka coast	0	200		28.52	shelf_slope	0-30	344
443	Heymans_1974_Wscotland_DeepSea	Scotland, Rockall Trough and its seamounts	376	2000		10.72	shelf_slope	30-58	347, 465
444	Heymans_1977_GulfMaine	Gulf of Maine and Georges Banks			150	10.93	shelf_slope	30-58	345
446	Hoover_1970_HudsonBay	Hudson Bay				0.07	bay	58-90	350, 351, 462
447	Hoover_1950_Antarctic	Antarctic Peninsula				-0.71	ocean	58-90	349, 463
448	Lees_1973_IrishSea	Irish Sea		150		11.28	shelf_slope	30-58	354
452	Libralato_2000_MNMR_Italy	Adriatic Sea, Gulf of Trieste, Miramare Natural Marine Reserve		18		17.40	coastal	30-58	180, 358
457	Mackinson_1991_NorthSea	North Sea		400	90	10.04	shelf_slope	30-58	362
461	Morissette_2000_WScotland	Scotland, Western	0	1000		10.72	shelf_slope	30-58	367

Number	Name	Location	Min depth	Max depth	Mean depth	SST	Ecosystem type	Latitude	Ref
462	Morissette_1995_NGulfStLawrence	Gulf of St Lawrence, Northern	37			4.42	shelf_slope	30-58	104, 366
465	Okey_1986_AlbatrossBay	Gulf of Carpentaria, Albatross Bay	0	40		27.93	bay	0-30	370
466	Okey_1990_GulfCarpentaria	Gulf of Carpentaria	0	70		27.85	bay	0-30	371
467	Okey_1995_SAtlanticBight	Atlantic Bight, Southern	0	500		24.97	shelf_slope	30-58	372
468	Orek_1990_BlackSea	Black Sea		2245	1271	14.86	shelf_slope	30-58	373
474	Piroddi_1964_NEIonianSea	Ionian Sea, North Eastern				19.57	shelf_slope	30-58	380
475	Piroddi_2007_NEIonianSea	Ionian Sea, North Eastern				19.57	shelf_slope	30-58	381
477	Preikshot_1950_StraitGeorgia	Strait of Georgia				10.66	shelf_slope	30-58	383
478	Preikshot_1950_BCShelf	British Columbia Shelf, Southern				10.37	shelf_slope	30-58	383
479	Preikshot_1950_NEPacific	Pacific Ocean, North Eastern				5.49	shelf_slope	58-90	383
485	Shannon_1978_SBenguela	Benguela, Southern				18.18	upwelling	30-58	389, 390, 522
486	Stobberup_1981_CapeVerde	Cape Verde Archipelago, Coastal ecosystem	0	200		24.25	shelf_slope	0-30	391
488	Tam_1997_NHumboldtCurrent	Humboldt Current Ecosystem, Northern				20.60	upwelling	0-30	392
489	Taylor_1996_SechuraBay	Sechura Bay		30	15	21.10	bay	0-30	393
490	Taylor_1996_IndependenceBay	Independence Bay		30	15	19.45	bay	0-30	394
495	Tsagarakis_2003_NAegeanSea	Aegean Sea, North	20	300		17.98	shelf_slope	30-58	397
496	Tsehaye_1998_Eritrea	Eritrea, Red Sea coast				29.02	reef	0-30	398
497	Valls_1998_PortCros	Port-Cros Archipelago	0	50		17.17	coastal	30-58	399
499	Wabnitz_2005_Honolulu_Kaloko	Honolulu, Kaloko-Honokohau		70		25.61	reef	0-30	403, 516
500	Watermeyer_1600_NBenguela	Benguela, Northern				17.02	upwelling	0-30	406
501	Watermeyer_1900_NBenguela	Benguela, Northern				17.02	upwelling	0-30	406
502	Watermeyer_1967_NBenguela	Benguela, Northern				17.02	upwelling	0-30	406
503	Watermeyer_1990_NBenguela	Benguela, Northern				17.02	upwelling	0-30	406

Number	Name	Location	Min depth	Max depth	Mean depth	SST	Ecosystem type	Latitude	Ref
504	Watermeyer_1600_SBenguela	Benguela, Southern				18.18	upwelling	30-58	407
505	Watermeyer_1900_SBenguela	Benguela, Southern				18.18	upwelling	30-58	407
513	Kay_2007_Liberia	Liberia shelf	0	200		27.95	shelf_slope	0-30	353
521	Field_1990_NCalifornianCurrent	Californian Current, Northern	0	1280		12.07	upwelling	30-58	302, 334
633	Bay of Biscay 1970	Bay of Biscay	0	1440		14.78	shelf_slope	30-58	13
634	Bay of Biscay 1998	Bay of Biscay	0	1440		14.78	shelf_slope	30-58	13
637	Central Chile 1998	Chile, central				14.63	upwelling	30-58	28
640	Coral Reef Mexican Caribbean	Mexico, Caribbean			6	27.89	reef	0-30	33
646	Guinee 1998	Guinea, large area off	0	5000		27.37	shelf_slope	0-30	50
650	Mauritania 1987	Mauritania EEZ				22.49	shelf_slope	0-30	85
651	Mauritania 1998	Mauritania EEZ				22.49	shelf_slope	0-30	85
654	Morocco 1984	Morocco, Atlantic coast				20.22	shelf_slope	0-30	90
655	Grand Banks of Newfoundland 1980s 2J3KL	Newfoundland	0	1000		4.76	shelf_slope	30-58	93, 526
663	South Orkneys/Georgia	Orkneys, Georgia, South				0.97	ocean	30-58	122
669	Upwelling Gulf of Salamanca	Gulf of Salamanca	10	200		27.48	upwelling	0-30	141, 142
674	Northern British Columbia 1950	British Columbia, Northern				10.00	shelf_slope	30-58	159, 172, 173
675	Northern British Columbia 2000	British Columbia, Northern				10.00	shelf_slope	30-58	159, 172, 173
677	Gulf of Nicoya	Gulf of Nicoya	0	200		28.29	bay	0-30	53
680	North Sea 1981	North Sea				10.04	shelf_slope	30-58	98
682	Bolinao Coral Reef	Santiago Island, Bolinao coral reef			2	28.22	reef	0-30	162
703	Tasmanian waters	Tasmania				14.56	shelf_slope	30-58	537
725	EwE6_Guinea2004_mai09_Reference	Guinea continental shelf	0	200		27.02	shelf_slope	0-30	523
726	EwE6_Guinea1985_dec07_Reference	Guinea continental shelf	0	200		27.02	shelf_slope	0-30	523

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Table F.2 Description of the two dimensions included in the principal component analysis (PCA): TL classes, associated correlation to the dimension, and p-value.

Dim 1			Dim 2		
TL	*correlation*	*p-value*	*TL*	*correlation*	*p-value*
4.3	0.969	0.00E+00	2.8	0.596	1.39E-13
4.2	0.969	0.00E+00	2.9	0.585	5.15E-13
4.4	0.964	0.00E+00	2.7	0.569	3.12E-12
4.1	0.960	0.00E+00	3	0.554	1.47E-11
4.5	0.955	0.00E+00	3.1	0.534	1.03E-10
4	0.945	0.00E+00	3.2	0.523	2.90E-10
4.6	0.943	0.00E+00	3.3	0.505	1.36E-09
4.7	0.929	0.00E+00	2.6	0.478	1.30E-08
3.9	0.923	0.00E+00	3.4	0.470	2.42E-08
4.8	0.915	0.00E+00	3.5	0.414	1.31E-06

Table F.3 Results of the Pairwise t-tests cross-comparing each ecosystem type mean log-transformed biomass to all other types. Numbers given correspond to the TL classes where a statistical difference (p-value<0.05) is observed ('*' indicates a p-value<0.1).

	bay	lagoon	reef	upwelling	shelf-trop
lagoon	4.5*/4.6/4.7/4.8/4.9/5/5.1/5.2/5.3/5.4/5.5				
reef	2.5/2.6/2.7/2.8*/3.3/3.4/3.5/3.6/3.7/3.8/3.9/4/4.1/4.2/4.3/4.4/4.5*	3.1*/3.2/3.3/3.4/3.5/3.6/3.7/3.8/3.9/4/4.1/4.2/4.3/4.4/4.5/4.6/4.7/4.8/4.9/5/5.1/5.2/5.3/5.4/5.5			
upwelling	2.5/2.6/2.7/2.8*/3.1*/3.2/3.3/3.4/3.5/3.6/3.7/3.8/3.9/4/4.1/4.2/4.3/4.4/4.5/4.6/4.7/4.8/4.9/5/5.1/5.2/5.3/5.4/5.5	2.9*/3/3.1/3.2/3.3/3.4/3.5/3.6/3.7/3.8/3.9/4/4.1/4.2/4.3/4.4/4.5/4.6/4.7/4.8/4.9/5/5.1/5.2/5.3/5.4/5.5	4.5*/4.6*/4.7/4.8/4.9/5/5.1/5.2/5.3/5.4/5.5		
shelf-trop	3.8*/3.9/4/4.1/4.2/4.3/4.4/4.5/4.6/4.7/4.8/4.9/5/5.1/5.2/5.3/5.4/5.5	3.9*/4/4.1/4.2/4.3/4.4/4.5/4.6/4.7/4.8/4.9/5/5.1/5.2/5.3/5.4/5.5	2.6/2.7/2.8/3.2*/3.3/3.4/3.5/3.6/3.7/3.8	2.6*/2.7/2.8/2.9/3*/3.1/3.2/3.3/3.4/3.5/3.6/3.7/3.8/3.9/4/4.1/4.2/4.3/4.4/4.5/4.6/4.7/4.8/4.9*	

	bay	lagoon	reef	upwelling	shelf-trop
shelf-temp	3.3/3.4/3.5/3.6/3.7/3.8/3.9/4/4.1/4.2/4.3/4.4/4.5/4.6/4.7/4.8/4.9/5/5.1/5.2/5.3/5.4/5.5	3.1/3.2/3.3/3.4/3.5/3.6/3.7/3.8/3.9/4/4.1/4.2/4.3/4.4/4.5/4.6/4.7/4.8/4.9/5/5.1/5.2/5.3/5.4/5.5	2.4*/4.7*/4.8*/4.9/5/5.1/5.2/5.3/5.4/5.5	3.3/3.4/3.5/3.6/3.7/3.8/3.9/4	3.1*/3.2/3.3/3.4/3.5/3.6/3.7/3.8/3.9*/4*/4.1/4.2/4.3/4.4/4.5/4.6/4.7/4.8/4.9/5/5.1/5.2/5.3*/5.4*/5.5*

Table F.4 Results of the Pairwise t-tests cross-comparing each ecosystem type mean log-transformed production to all other types. Numbers given correspond to the TL classes where a statistical difference (p-value<0.05) is observed ('*' indicates a p-value<0.1).

	bay	lagoon	reef	upwelling	shelf-trop
lagoon	4.6*/4.7/4.8/4.9/5/5.1/5.2/5.3/5.4/5.5				
reef	2.5*/2.6/2.7/3.3*/3.4/3.5/3.6/3.7/3.8/3.9/4/4.1/4.2/4.3*	3.1/3.2/3.3/3.4/3.5/3.6/3.7/3.8/3.9/4/4.1/4.2/4.3/4.4/4.5/4.6/4.7/4.8/4.9/5/5.1/5.2/5.3/5.4/5.5			
upwelling	2.5/2.6/2.7/3.4/3.5/3.6/3.7/3.8/3.9/4/4.1/4.2/4.3/4.4/4.5/4.6/4.7/4.8/4.9/5/5.1/5.2/5.3/5.4/5.5	3.1*/3.2/3.3/3.4/3.5/3.6/3.7/3.8/3.9/4/4.1/4.2/4.3/4.4/4.5/4.6/4.7/4.8/4.9/5/5.1/5.2/5.3/5.4/5.5	4.5*/4.6*/4.7*/4.8/4.9/5/5.1/5.2/5.3/5.4/5.5*		
shelf-trop	3.9*/4.1/4.2/4.3/4.4/4.5/4.6/4.7/4.8/4.9/5/5.1/5.2/5.3/5.4/5.5*	3.3*/3.4*/3.8*/3.9/4/4.1/4.2/4.3/4.4/4.5/4.6/4.7/4.8/4.9/5/5.1/5.2/5.3/5.4/5.5	2.6*/2.7*/3.3/3.4/3.5/3.6*	2.4*/2.5/2.6/2.7/3.3*/3.4/3.5/3.6/3.7/3.8/3.9/4/4.1/4.2/4.3/4.4/4.5*/4.6*/4.7*/4.8*	
shelf-temp	3.7*/3.8/3.9/4/4.1/4.2/4.3/4.4/4.5/4.6/4.7/4.8/4.9/5/5.1/5.2/5.3/5.4/5.5	3.2/3.3/3.4/3.5/3.6/3.7/3.8/3.9/4/4.1/4.2/4.3/4.4/4.5/4.6/4.7/4.8/4.9/5/5.1/5.2/5.3/5.4/5.5	5.4*/5.5*	2.4/2.5/2.6/2.7/3.4*/3.5/3.6/3.7/3.8/3.9/4/4.1/4.2*	

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Table F.5 Results of the Pairwise t-tests cross-comparing each ecosystem type mean log-transformed kinetic to all other types. Numbers given correspond to the TL classes where a statistical difference (p-value<0.05) is observed ('*' indicates a p-value<0.1).

	bay	lagoon	reef	upwelling	shelf-trop
lagoon					
reef					
upwelling	2.5/2.6*	2.3*	2/2.3/2.4/2.5		
shelf-trop			2	2.3/2.4/2.5/3.2*/ 3.3*/3.4*	
shelf-temp			5.1*/5.2/5.3/5.4/ 5.5	2/2.3/2.4/2.5/2.6 /5*/5.1*/5.2/5.3/ 5.4/5.5	2/3.5*/3.6/3.7/3.8/ 3.9/4/4.1/4.2/4.3/4 .4/4.5/4.6/4.7/4.8/ 4.9/5/5.1/5.2/5.3/5 .4/5.5