UNDERSTANDING, MODELING AND PREDICTING TROPHIC INTERACTIONS BETWEEN MARINE SPECIES

by

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Abstract

In this thesis, I explore and propose new methodologies and intend to provide new insights for understanding, modeling and predicting trophic interactions between marine species. I introduce the importance of trophic interactions in marine ecosystems and the common ecosystem modeling approaches applied to marine food webs. First, I present an attempt to synthetize information from all published Ecopath with Ecosim (EwE) models worldwide, gathered in the EcoBase digital repository. Through the compilation and standardization of a suite of metadata, I describe and discuss the usage of the EwE modeling approach and its evolution over time, since its very first application. I also present a meta-analysis of Ecopath models based on these metadata, where I select the models of potential interest, using a scoring method, and focus on one particular aspect of food web modeling, relating to the identification of keystone species. I propose a comprehensive and critical review of the ill-defined concept of keystone species and argue for a restored, exclusive and operational definition of the concept. The proposed definition is placed in a larger framework that considers different categories of ecologically important species. Then, a new functional index of keystoneness is derived from the EwE modeling approach, so as to identify potential keystone species in marine food webs. The proposed index addresses some of the biases observed in previously applied indices. Finally, I present an attempt to predict diet composition for predatory fish species. The intention is to build on existing large datasets, provided in the FishBase biodiversity information system, to identify predictors of fish feeding selectivity. The determination of clear or consistent pattern between biological and ecological species straits and diet composition is challenged by data restrictions, but some recommendations for future studies are provided. In conclusion, data availability may be a critical issue when considering some aspects of trophic interactions, especially for modeling and predictions at the species level. Data sharing within the scientific community, notably through the use of digital and open-access information repositories, is critical for the development of global meta-analyses in marine ecology.

Preface

With the exception of Chapters 1 and 6, all of the chapters in this dissertation have been prepared as stand-alone, peer-reviewed publications. Chapters 2 and 3 are under review at refereed journals, while Chapter 4 is in press. Chapter 5 is in preparation for submission. I am the senior author on all of the papers, and I led the design, implementation, analysis and writing of all co-authored chapters. Details of co-authorship contributions are stated below.

Chapter 2 is co-authored by Mathieu Colléter, Jérôme Guitton, Didier Gascuel, Daniel Pauly, and Villy Christensen. Mathieu Colléter and Didier Gascuel initiated the project of EcoBase. I initiated this study, following my collaboration with Mathieu Colléter on the production of a scientific report introducing EcoBase. I share first authorship with Mathieu Colléter on this study, to which we equally contributed regarding the design of the study, collection of the information, analysis of the data and writing of the manuscript. Jérôme Guitton assisted with technical issues with the development and use of the EcoBase database. Didier Gascuel, Daniel Pauly, and Villy Christensen provided edits, comments, and suggestions on the manuscript. A version of this chapter is under review.

Chapter 3 is co-authored by Marta Coll and Villy Christensen. Marta Coll suggested the idea of a literature review. I expanded on the original idea and conducted a more in-depth review than originally envisaged. I reviewed the literature and wrote the manuscript. Marta Coll contributed to this chapter through stimulating discussions and suggestions on drafts of the manuscript. Villy Christensen provided guidance throughout the development of the manuscript. A version of this chapter is under review.

Chapter 4 is co-authored by Marta Coll and Villy Christensen. The original idea and its conceptualization for this chapter are mine. I developed the methods, carried out all analyses and prepared the manuscript. Marta Coll provided data, methodological guidance on statistical analyses, and contributed to this chapter through stimulating discussions and suggestions on drafts of the manuscript. Villy Christensen provided guidance throughout the development of the manuscript. A version of this chapter is in press in *Ecological Monographs*.

Chapter 5 is co-authored by Deng Palomares and Villy Christensen. I designed the study, conducted the analyses and prepared the manuscript. Deng Palomares assisted with the use of the FishBase database, and contributed to this chapter through stimulating discussions and comments on drafts of the manuscript. Villy Christensen suggested the original idea of this chapter and provided guidance throughout the development of the manuscript. A version of this chapter is in preparation for submission.

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Dedication

To my grandparents: Jean & Amparo and Jean & Jacqueline

1. Introduction

1.1. Context

It is a general perception that the oceans are the last frontier and that we have but scratched the surface when it comes to understanding how marine ecosystems function as well as what life they shelter. This is in many respects true, but we also have gathered considerable information about life in the world's oceans. About 226,000 marine species have been described, and 58,000 to 72,000 species have been sampled but not yet described, for a predicted total of 0.7 to 1.0 million marine species (Appeltans et al. 2012). Previous higher estimates are now considered unlikely (Appeltans et al. 2012, Costello et al. 2013). Moreover, the number of described species have been increasing over the last decade, so that most species could be discovered by the end of the century (Appeltans et al. 2012, Costello et al. 2013). In comparison, the total number of species on the planet was estimated to be about five millions, with a three millions error margin, and of which 1.5 million were valid described species (Costello et al. 2013).

The world's oceans are dynamic systems, which undergo different types of changes, from species extinctions, population declines or habitat degradations to species invasions (Sala and Knowlton 2006). In a recent review (including about 80 species or groups of species from various marine environments), the percent of population decline ranged from 39% for crustaceans to 91% for oysters, with most of the mammals, birds, and reptiles severely depleted by 1900 and even further by 1950 (Jackson 2008). Other studies demonstrated that the biomass of large predatory fish has declined by two-thirds from 1950 to 1999 in the North-Atlantic (Christensen et al. 2003b), and globally by two-thirds over the last hundred years (Christensen et al. 2014a). Habitat-forming species in the coastal zones, such as corals, mangroves or seagrasses, were estimated to be critically endangered on a global scale, with a reduction percentage ranging from 50 to more than 90% (Jackson 2008).

1.1.1. Drivers of changes in marine ecosystems

There are several natural factors causing changes in marine ecosystems. First, natural variability may be caused by modifications in physical processes, either due to external factors such as solar radiation, or due to internal factors, such as ocean-atmosphere interactions. Natural variability may also be induced by biological processes, such as the combined effect of bottom-up and top-down controls. Bottom-up or resource control corresponds to the regulation of ecosystems by variability in primary production or nutrient inputs, while top-down control corresponds to the regulation by predation (Pace et al. 1999).

Anthropogenic factors also represent strong drivers of change in marine ecosystems and food webs (Sala and Knowlton 2006, Halpern et al. 2008). Indeed, marine species within a given habitat are adapted to natural pulse disturbances, but not necessarily to human-made chronic disturbances (Gray 1997, Sala and Knowlton 2006). Halpern *et al.* (2008) showed that no area of the world's oceans is unaffected by anthropogenic impact, and that 41% is strongly affected by multiple human activities. Moreover, synergistic effects of combined human activities make human impacts on marine ecosystems stronger, while potential thresholds effects make them unpredictable (Jackson et al. 2001, Folke et al. 2004, Sala and Knowlton 2006). 'Regime shifts', i.e. changes from one rather stable condition or 'state' to another, have been observed in marine ecosystems and were associated with different human-induced causes (Scheffer et al. 2001, Knowlton 2004, Daskalov et al. 2007). According to demographic projections, global human population will increase up to nine billions by 2050 (ten Brink 2010). Thus, under current conditions, human pressure on marine ecosystems is likely to increase as well, especially in coastal areas where human population is concentrated (Martínez et al. 2007).

The two main globally-distributed anthropogenic drivers impacting marine ecosystems are commercial fishing and human-induced climate change (Halpern et al. 2008). Commercial fishing may have significant impacts on marine ecosystems if it occurs above sustainable levels and leads to overfishing. For instance, overfishing was identified as the main cause of disturbance and collapse in coastal ecosystems (Jackson et al. 2001). Human-induced climate change designates the perturbation of natural variability in oceanic physical, biological and chemical conditions, driven by increasing greenhouse gases (notably carbon dioxide) emissions from human activities (Doney 2010). In addition to overexploitation and anthropogenic climate

change, species introductions and water pollution (contamination and eutrophication), caused by human activities (e.g., shipping, fertilizer use) also represent important threats to marine biodiversity (Sala and Knowlton 2006, Costello et al. 2010).

1.1.2. Impacts of fishing on marine ecosystems

Fishing activities exert significant impacts on marine ecosystems and biodiversity worldwide (Pauly et al. 2002). Indeed, overfishing causes serious depletions worldwide (Pitcher and Cheung 2013). Overall, global capture fish production in marine waters have remained steady since the 1980s (FAO 2014). However, when considering the increase in fishing power, the efficiency of the world's fisheries (i.e. landings/effort) actually shows a reduction by half since the 1950s (Watson et al. 2013). While well-assessed fisheries may be moving toward sustainable exploitation patterns, unassessed stocks show continued decline due to overfishing (Costello et al. 2012). The fraction of overfished stocks (i.e. stocks exploited at biologically unsustainable levels) has increased over the last decades, up to nearly 30 percent in 2011, while the proportion of fully fished stocks accounted for about 60 percent of the total number of stocks assessed (FAO 2014).

Fishing activities are responsible for population declines of target species, but also of non-targeted species through by-catch, i.e. incidental catch or discards (Hall et al. 2000). Marine mammals, sea birds, and sea turtles are the most severely impacted species due to incidental mortality (Hall et al. 2000). Shrimp trawls and bottom trawls are the fishing gears that have the highest amount of by-catch (Pitcher and Cheung 2013). Moreover, when used on sensitive habitats, such as seagrass or coral beds, bottom trawls represent one the most destructive fishing practices (Pitcher and Cheung 2013). Thus, in benthic and deep-sea marine ecosystems, chronic disturbance from trawl fishing leads to the removal of seabed species, lower productivity and fragmentation of the habitat they form (Kaiser et al. 2002).

Severe and continuous declines may result in the extinction or collapse of overfished populations (Casey and Myers 1998, Sadovy and Cheung 2003). Large, long-living and slowly maturing species, such as sharks (Stevens et al. 2000), are more particularly threatened with extinction (Sadovy 2001). Of the 133 local, regional, and global extinctions of marine populations documented worldwide, 55% were caused by unsustainable exploitation, and 37%

driven by habitat loss (Dulvy et al. 2003). Even when not spatially extinct, a species may become functionally or ecologically extinct, when it becomes so rare that it no longer fulfills its function in the ecosystem (Carlton et al. 1999, Sala and Knowlton 2006). Ecological extinction may be due to over-exploitation, such as for sea otters in the Northeast Pacific, baleen whales in the Southern oceans, or the Newfoundland cod (Carlton et al. 1999, Jackson 2008).

Fishing activities initially targeted valuable, large predatory fish species, located at the upper end of marine food webs. However, as the populations of large predators progressively became depleted by overfishing, targeted species were gradually replaced by less valuable, smaller foraging fish species, a phenomenon known as 'fishing down marine food webs' (Christensen 1996, Pauly et al. 1998). This shift in fish stocks composition was revealed by the decline of the mean trophic level of global fisheries catch (Pauly et al. 1998, Pauly and Palomares 2005, Pauly and Watson 2005), which has been observed in many regions of the world (Stergiou and Christensen 2011). More generally, the loss of large apex consumers due to human influence on nature, also called 'trophic downgrading', has been observed worldwide, both in aquatic and terrestrial ecosystems (Estes et al. 2011). The direct consequence of humaninduced removal of top predator species is a simplification of the food web, which may lead to major shifts in the ecosystem structure and dynamics (Pauly et al. 2002, Estes et al. 2011). In addition, by targeting the larger individuals, fishing selects for individuals that grow slower and reproduce earlier and at smaller sizes (Conover and Munch 2002). Thus, due to phenotypic plasticity, fishing induces changes in the size distribution and the life-history traits of exploited fish stocks, and may thus impact their evolutionary characteristics and lead to genetic diversity loss in the long term (Gray 1997, Law 2007). Overall, the disturbance of marine ecosystems caused by fishing activities may amplify the impacts of environmental variability (Pauly et al. 2002, Sala and Knowlton 2006, Estes et al. 2011).

1.1.3. Effects of climate change on marine ecosystems

Climate change modifies the ocean biogeochemistry by inducing warming, acidification and deoxygenation (the loss of dissolved oxygen from the ocean) (Doney 2010, Gruber 2011). These three processes interact, creating synergistic effects, and occur at the global scale, but with distinct regional patterns (Gruber 2011). Changes in environmental conditions impact marine organisms and ecosystems in various and complex ways (Hoegh-Guldberg and Bruno 2010, Doney et al. 2012). New environmental conditions may be tolerable if they do not alter species' physiological performance. Tolerance corresponds to the persistence *in situ* of a marine species in response to climate change (Dawson et al. 2011), and involves either acclimatization, i.e. adjustment of individuals physiology, or adaptation, i.e. natural selection of tolerant genotypes over generations (Parmesan 2006, Doney et al. 2012). When climate change creates intolerable conditions, species may show different modes of response: change in geographic range (either depth range, i.e. by habitat shift, or latitudinal range, i.e. migration), change in phenology (timing of annual events), or local extinction (Parmesan 2006, Dawson et al. 2011, Doney et al. 2012).

The best-documented biological impacts are shifts in the abundance and distribution of populations due to water temperature increase (e.g., Perry et al. 2005, Nye et al. 2009, Raitsos et al. 2010). Projections of global marine species distributions under climate change scenarios predicted pole-ward migration of species, leading to local climate-driven extinctions or invasions (Cheung et al. 2009). Indeed, fish have the tendency to remain in the same temperature ranges, and so respond to climate change by moving so as to stay where the temperature is tolerable (Pauly 2010). Nevertheless, changes in ocean chemistry, and notably ocean acidification, may be more important than ocean warming for the physiological performance of many organisms (Harley et al. 2006). For instance, the ability of corals to maintain their external calcium carbonate skeletons is directly affected by seawater CO₂ chemistry (Orr et al. 2005, Fabry et al. 2008). Global ocean warming and acidification lead to mass coral bleaching and mortality threatening coral reef communities and ecosystems (Hoegh-Guldberg et al. 2007). Moreover, while higher water temperature or acidity increases oxygen demand for growth in fish (and other heterotrophic organisms) (Pörtner and Knust 2007, Pörtner 2008), ocean deoxygenation reduces oxygen supply and creates oxygen minimum zones (Keeling et al. 2010). As a result, climate change may increase aerobic stress for fish, which in turn may modify their feeding behavior and affect their growth and reproduction (Pörtner and Knust 2007, Pauly 2010). Thus, assemblageaveraged maximum body weight of fishes is projected to decrease by 14 to 24% globally from 2000 to 2050 under climate change scenarios (Cheung et al. 2012).

In response to warming, acidifying, and stratifying oceans, marine ecosystems also show: decreasing primary production with potential consequences on nutrient input (Polovina et al. 2008, Steinacher et al. 2010); changes in ocean circulation driving population dynamics through larval dispersal (Harley et al. 2006); and increasing sea-level rise causing coastal habitat loss (Hoegh-Guldberg and Bruno 2010). All these climate-induced changes in marine species, populations, or communities may have consequences on ecosystem properties, such as biodiversity or food-web structure, notably through the disturbance of material and energy flows and biogeochemical cycles (Doney et al. 2012). For instance, the 'match-mismatch' hypothesis corresponds to a trophic asynchrony in the climate-induced phenological changes between interacting predator and prey populations (Cushing 1990, Edwards and Richardson 2004, Durant et al. 2007). As a result, global drivers of climate change have significant impacts on marine ecosystem functions and services (Doney et al. 2012). For instance, large-scale redistribution of global fisheries catch potential for exploited marine species was predicted under climate change scenarios (Cheung et al. 2008, Cheung et al. 2010, Cheung et al. 2011), with potential impacts on fisheries economics worldwide (Sumaila et al. 2011).

1.1.4. Consequences on marine ecosystems functions and services

Ecosystem functions designate the ecological processes regulating the fluxes of energy, nutrients and organic matter in the ecosystem, while ecosystem services describe the suite of benefits that ecosystems provide to humanity (Cardinale et al. 2012). Examples of marine ecosystem services notably encompass seafood supply, protection against erosion or extreme events, recycling of pollutants (Sala and Knowlton 2006). Biodiversity controls basic ecosystem functions, directly influences certain provisioning and regulating ecosystem services, and may be considered as an ecosystem service (Cardinale et al. 2012, Mace et al. 2012). For instance, greater fish diversity strongly correlated with higher fisheries yields and productivity (Bracken et al. 2007), and was associated with greater stability of fisheries yields (Cardinale et al. 2012). However, anthropogenic drivers of changes in the oceans have caused a rapid decline in global marine biodiversity, with subsequent consequences on marine ecosystem functions and services (Sala and Knowlton 2006). Globally, indicators of the state of biodiversity show declines, with no significant recent reductions in rate, whereas indicators of pressures show increases (Butchart et al. 2010). Moreover, biodiversity loss may significantly alter ecosystem functions and services globally, so that it could be a major driver of ecosystem change (Cardinale et al. 2012, Hooper et

al. 2012). Thus, while seafood demand is increasing worldwide and food security issues are rising, marine biodiversity loss is a serious concern to human societies (Rice and Garcia 2011).

In addition, marine ecosystems provide multiple services, which may involve trade-offs between the supplies of different services. Indeed, simplifying ecosystems may optimize certain provisioning services locally and temporary, but may also lead to biodiversity loss, and thus reduce regulating services on larger scales and in longer terms (Pereira et al. 2010, Cardinale et al. 2012). The loss of individual species may have indirect ecosystem-wide impacts, especially for species playing important functional roles in marine ecosystems (Sala and Knowlton 2006). Thus, the removal of top predators caused by overexploitation in marine ecosystems impacts functional diversity and has effects on a wide range of ecosystem processes (Estes et al. 2011, Cardinale et al. 2012). Another example is the predicted loss of coral reefs and its consequences on coastal protection, fisheries and tourism activities (Hoegh-Guldberg et al. 2007).

1.2. Concepts and definitions

1.2.1. Marine biodiversity

Biodiversity is usually shorthanded for biological diversity, defined by the Convention on Biological Diversity as "the variability among living organisms from all sources [...] and the ecological complexes of which they are a part". In other words, biodiversity encompasses the variety of life forms including plants, animals and microorganisms, the genes that they contain and the ecosystems that they form. Biodiversity can be subdivided into terrestrial, freshwater or marine biodiversity, by distinguishing the main types of ecosystems occurring on Earth. Thus, marine biodiversity represents the variety of life in the oceans (Sala and Knowlton 2006).

Biodiversity is a multi-faceted concept, comprising four main aspects: compositional diversity, which measures the number of entities (or richness); structural diversity, which measures the distribution of abundance of the entities (or evenness); functional diversity, which measures the functional roles the entities play in ecosystems; and what we could call 'differential' diversity, i.e. a measure of the differences among species (e.g., morphological disparity or genetic divergence) (Sala and Knowlton 2006). Entities may consist of genes or

individuals, species, communities or ecosystems, depending on the chosen resolution of the biodiversity concept. A species may comprise one or more populations, i.e. groups of individuals that can reproduce and interchange genetic material, while a community corresponds to a group of species co-occurring under the same environmental conditions (Gray 1997). The most commonly used metric of biodiversity is the species and its most common measure is species richness, i.e. the number of species found in a given area (Gotelli and Colwell 2001).

Changes in marine biodiversity can be considered over different temporal scales: the evolutionary timescale (i.e. over many generations); or the ecological timescale (i.e. over few generations) (Gray 1997, Sala and Knowlton 2006). Over evolutionary timescales, marine biodiversity has been increasing, apart from some mass extinction events, and its recovery capacity has not been reduced (Sala and Knowlton 2006). Over ecological timescales, human activities have caused more rapid changes to marine biodiversity than the natural changes caused by ecological succession (Sala and Knowlton 2006). Anthropogenic impacts might be outcompeting natural processes in such a way that the term 'Anthropocene' has recently been popularized to describe the current geological epoch (Crutzen and Steffen 2003, Steffen et al. 2007, Rockstrom et al. 2009). In addition, marine biodiversity can be measured at different spatial scales (Gray 1997). At local scales, within-habitat (or alpha) diversity is defined for a given sampled ecosystem or community, and between-habitat (or beta) diversity when sampling covers more than one ecosystem or community. From regional to global scales, landscape (or gamma) diversity is defined as the mosaic of ecosystems or communities over larger samples. Within-species (or point) diversity can also be defined when considering a smaller sample consisting of a single species (Sala and Knowlton 2006).

1.2.2. Trophic interactions

Trophic interactions designate feeding relationships between organisms and may be described using food webs, trophic pyramids, flow diagrams, or trophic spectra. Food webs are maps representing the linkages between predator and prey species in the community (Pimm et al. 1991, Menge 1995). Trophic pyramids are diagrams where producers and consumers are arranged according to their size, number and production rate (Lindeman 1942). Based on trophic pyramids, Lindeman (1942) introduced the concept of trophic level, which is the position of an

organism in the food web, determined by its feeding preferences. Seeing that most marine organisms function at several trophic levels, fractional trophic levels were then defined (Odum and Heald 1975). Thus, using trophic levels, functional biodiversity can be characterized in two principal dimensions, horizontal and vertical: horizontal diversity considers diversity within a single trophic level, while vertical diversity considers diversity across trophic levels (which may be measured by the degree of omnivory or the food-chain length) (Duffy et al. 2007). Flow diagrams are graphical representations of trophic interactions in food-web models. Organisms are arranged based on their trophic level and interconnected boxes or nodes are used to represent their biomass and trophic flows (e.g., Christensen et al. 2008). An ecosystem may also be represented by the distribution of one of its descriptive parameter (such as biomass) across trophic levels, called the (biomass) trophic spectrum (e.g., Gascuel et al. 2011).

Trophic interactions may have direct or indirect effects, through changes in species abundance (Menge 1995). Direct effects are defined as the influence of a species on another species resulting from their direct interaction, while indirect effects correspond to the influence of a species on another species with which it does not interact directly (Menge 1995). Direct effects caused by trophic interactions correspond to predation, while several types of indirect effects may be due to trophic interactions, such as: (i) 'keystone predation', when a predator indirectly increases the abundance of competitors of its prey via consumption of the highly competitive prey; (ii) 'trophic cascade', when an increase in abundance is caused by the control of predator by a predator of the predator, i.e. it is an effect over three trophic levels; (iii) 'exploitation competition', when the reduction of a consumer is caused by reduction of its prey by another consumer; (iv) 'apparent competition', when a reduction of a prey is caused by the increase of another prey which enhances predation by a common predator (Holt 1977); and (v) 'habitat facilitation', when a species indirectly improves the habitat of another species by reducing the abundance of a third species which has a negative effect on this habitat (Menge 1995). Keystone predation was identified as the most common type of indirect effect in rocky intertidal habitats, while apparent competition and trophic cascades were also common (Menge 1995). Trophic cascades were originally assumed to be more common in pelagic communities, whereas keystone predation would be more common in benthic communities (Menge 1995). Subsequent studies suggested that trophic cascades were not restricted by the type of ecosystems, but were less likely under certain biotic or abiotic conditions (Pace et al. 1999). In fact, trophic

cascades have now been documented in both benthic and pelagic marine ecosystems (Verity and Smetacek 1996, Pinnegar et al. 2000), as well as in terrestrial and freshwater ecosystems (Estes et al. 2011).

The importance of a trophic interaction, called 'interaction strength', is defined by the magnitude of its effect on the community (Paine 1980, Menge 1995). A strong interactor species has a large effect on the species with which it interacts, while a weak interactor species has a small effect on the other species (Paine 1980, Menge and Freidenburg 2001). A reduction in the abundance of a strong interactor may induce community-wide changes and affect many other species, through the disturbance of trophic interactions (Paine 1980, Sala and Knowlton 2006). In contrast, changes caused by the depletion of weak interactors may be unpredictable (Sala and Knowlton 2006). Due to their strong influence on the food-web structure of the community, strongly interacting species may be defined as critical species or 'ecologically important species' (Perry 2010). Several types of critical species may be discriminated based on their role and position in the food web. At the top of the food web, 'keystone' species correspond to strongly interacting species of high trophic level whose trophic impacts are disproportionately large relative to their abundance (Paine 1966, 1969a). Lower in the food web, 'key-industry' species correspond to species of intermediate trophic level that act as trophic links between primary producers and top predators (Elton 1927). At the bottom of the food web, 'foundation' species, such as abundant primary producers, also contribute to the maintenance of the food-web structure of the community (Dayton 1972, Ellison et al. 2005).

1.2.3. Diet composition

In quantitative food-web analyses, trophic interactions are defined using the diet composition (DC) of species. DC corresponds to the proportion of each prey in the diet of a predator (Christensen and Walters 2004). DC should ideally be expressed in weight or volume, so that trophic relationships may be determined in energetic terms (Stobberup et al. 2009). Fish species' diet composition is commonly derived from stomach contents data, which are complex, time-consuming, and expensive to collect (Link 2004, Albouy et al. 2011). The main difficulty in stomach contents analysis is the taxonomical identification of all species remains. Thus, diet composition data is often very scarce in the literature, either available for well-known fish

species only, or lacking taxonomic details. When no data is available, DC is either derived from data on similar species in the literature, or arbitrary defined based on expert knowledge. DC is sometimes assumed to be equal to prey relative abundance, although the relative abundance of prey is not a good predictor of diet composition for fish species (Link 2004). As a consequence, DC is usually one of the most poorly estimated parameters in quantitative food-web analyses (Link 2004).

Most fish are generalist feeders, that feed on a broad range of prey items (Gerking 1994). Besides, fish commonly are opportunists when they feed, i.e. they take advantage of available sources of food in their environment (Gerking 1994, Link 2004). Thus, in absence of data, predicting fish diet composition may be challenging. Nevertheless, when several prey items are available, fish select certain prey items among all available based on some constraints. The challenge is to identify the main constraints that influence fish feeding selectivity. Size is known as a key parameter to determine predator-prey interactions (Cohen et al. 1993, Thiebaux and Dickie 1993, Gill 2003), but characteristics other than size may influence prey preference and utilization for fish species (Gerking 1994, Link 2004). Prey preference may be defined as the favored choice of the predator for the most suitable prey items, whereas prey utilization (or diet composition) corresponds to the realized preference, coupled with prey availability (Link 2004).

In a few cases, fish diet compositions were predicted based on a suite of characteristics describing predator and prey species (e.g., Sibbing and Nagelkerke 2001, Link 2004). Yet, there is no strong consensus in the literature on good predictors of fish diet composition. Based on the ecomorphological hypothesis of a correlation between species morphology and ecology, the morphology of the feeding apparatus could be a good predictor of prey utilization for fish (Motta et al. 1995, Norton 1995). However, there is contrasting evidence from the literature to verify the hypothesis of dietary-morphological relationships in fish. In many cases, the ecomorphological traits could be used to predict some general aspects of fish feeding only (i.e. trophic guilds, e.g., Boyle and Horn 2006, Ibañez et al. 2007, Oliveira et al. 2010, Albouy et al. 2011). Fish morphology may predict the way fish are feeding (prey preference or feeding mode), but not the prey they feed on (prey utilization or diet composition) (Motta 1988, Motta et al. 1995, Clifton and Motta 1998, Barnett et al. 2006).

1.3. Methods and approaches

1.3.1. Ecosystem-based management

Ecosystem-based management (EBM) has become one of the key policy objectives in the strategic plans of international organizations (Link and Browman 2014). Ecosystems were defined by the Convention on Biological Diversity as "a dynamic complex of plant, animal and micro-organism communities and their non-living environment interacting as a functional unit". According to this definition, ecosystem-based management should consider the whole food web, as well as the abiotic factors that influence it (Link 2002b). A more recent definition described ecosystems as a geographically specified system including biotic and abiotic factors, but also humans (Francis et al. 2007). In fact, EBM aims at considering and addressing the multiple, simultaneous, and sometimes cumulative, natural and anthropogenic pressures faced by the important components of ecosystems (Link and Browman 2014). The implementation of EBM for marine ecosystems requires integrated assessments, which can be applied to different oceanuse sectors and adopted at different levels: (i) EBM integrate all sectors of activities over all levels of management; (ii) ecosystem-based fisheries management (EBFM) uses integrated ecosystem assessments with a focus on the fisheries sector; and (iii) ecosystem approach to fisheries (EAF) focuses on fisheries stocks with some ecosystem considerations (Link and Browman 2014).

Interest in ecosystem-based management in the fisheries sector notably rose from issues related to conflicting stakeholders, debate over the most important ecosystem processes, and limitations of traditional single-species management (Link 2002b). Indeed, fisheries management occur in a broadly interdisciplinary context, involving biological, ecological, oceanographic, social, and economic aspects (Link 2002b). Moreover, there has been a recognition that ecosystems provide services beyond the scope of fisheries management (i.e. the targeted stock) and that fishing impacts these services via habitat degradation, incidental mortality of non-targeted species, changes in targeted populations, and disturbance of food webs (Link 2002b, Pikitch et al. 2004). Thus, facing the inherent complexity of natural ecosystems, a more effective and holistic approach was needed to prioritize and maintain the ability of ecosystems to produce these services (Link 2002b, Pikitch et al. 2004). The objective of EBFM

is to manage the conditions in the ecosystem that maintain critical processes for the persistence of the desirable ecosystem state (Link 2002b), by "reversing the order of management priorities to start with the ecosystem rather than the target species" (Pikitch et al. 2004). In the context of EBFM, ecosystem models (EM) were one of the tools used to evaluate ecosystem properties and give insights on the potential effects that changes in management practices would have on ecosystems (Christensen and Walters 2005, Christensen and Walters 2011, Espinoza-Tenorio et al. 2012).

1.3.2. Ecosystem models

Models are coherent and purposeful representations of systems and of the processes therein, and may consist of words, graphs or equations, which describe the system elements and their relationships with the surrounding environment (Starfield et al. 1990, Pauly and Christensen 2002). Mathematical models representing marine ecosystems may be classified into different types, based on their characteristics and objectives. First, we can discriminate statistical or empirical models from process-based or mechanistic models (Whipple et al. 2000). Statistical models encompass exploratory models and analytical models, the latter type corresponding to (single-species, structured or not) stock assessment models (SAM) (Whipple et al. 2000). Another category described as extended stock assessment models (ESAM, taking a few additional species interactions into account) may be included in statistical models (Plagányi 2007, Hunsicker et al. 2011). Statistical models are used to detect potential patterns using frequentist or Bayesian approaches to probability, and provide algorithms and parameters used in process-based models (Whipple et al. 2000). Process-based models may be sub-categorized into qualitative and quantitative models. Qualitative process-based models describe qualitative interactions between the elements of the system and include: (i) food web models, i.e. unsigned directed graph models; and (ii) loop analysis models, i.e. signed diagraph models (Whipple et al. 2000, Fulton 2010). Although substantial insights into ecosystem functioning may be gained from qualitative models, whose implementation is rapid and flexible, the development and implementation of process-based models within the framework of EBFM has mainly focused on quantitative modeling approaches (Fulton 2010).

Quantitative process-based models correspond to the main models used in fisheries and ecosystem modelling today, ranging from minimal realistic models to whole system models (Hunsicker et al. 2011). They comprise multi-species models, 'ecosystem models', and 'end-toend models'. Multi-species models (MSM) correspond to the multi-species versions of stock assessment models (Hollowed et al. 2000, Whipple et al. 2000, Pauly and Christensen 2002), such as multi-species virtual population analysis (MSVPA) (Magnusson 1995), or models based on the Lotka-Volterra equations (May et al. 1979). MSMs focus on a limited number of species, the ones that have important interactions with the target species (Plagányi 2007). In contrast, ecosystem models (EM) may be defined as models that attempt to represent all biological components of the ecosystem (i.e. the entire food web) (Whipple et al. 2000, Plagányi 2007). EMs may be static if developed for descriptive purpose, or dynamic and predictive. Components of EMs may be defined as individuals, species, or groups of species. Species-based ecosystem models include trophic flow models (e.g., Prognostic Bulk Biomass (PROBUB) and Dynamical Numerical Marine Ecosystem Simulation (DYNUMES) models for the Bering Sea (Laevastu and Larkins 1981), Ecopath with Ecosim (EwE) models (Christensen and Pauly 1992, Pauly et al. 2000, Christensen and Walters 2004)) and ecological network analyses (e.g., Netwrk (Ulanowicz and Kay 1991, Ulanowicz 2004)). Individual-based models (IBM) use decision algorithms to simulate the behaviour of individuals so as to understand system properties and dynamics (Grimm and Railsback 2005). EMs may use specific metrics, such as size or trophic level. Size spectra models represent the ecosystem as a continuous distribution of biomass per body mass class, with biological rates and feeding interactions determined by size ratios (Jennings et al. 2008). Similarly, trophic spectra models represent the ecosystem as a continuous distribution of biomass per trophic level class (e.g., EcoTroph (Gascuel 2005, Gascuel and Pauly 2009, Gasche and Gascuel 2013)).

End-to-end models (E2EMs) (or whole system models) are the last generation of marine ecosystem models, that attempt to represent the entire ecosystem, including biological, physical and human components, allowing for two-way coupling between them, and integrating both bottom-up and top-down controls (Travers et al. 2007, Fulton 2010, Rose et al. 2010). E2EMs may be inappropriate tools for tactical management, but useful for answering system-level 'what-if' management questions or testing impact scenarios (Fulton 2010). E2EMs may correspond to network-based models (e.g., Ecopath with Ecosim (EwE), see Section 1.3.3) or Agent-Based Models (ABM) (individual-based models allowing different types of individuals, such as InVitro (Fulton 2010)). Some E2EMs, such as the NEMURO-FISH (Rose et al. 2007) or ATLANTIS (Fulton et al. 2011) models, are coupled with a biogeochemical model. Another subcategory of E2EMs consist of hybrid models, i.e. models created by coupling different types of models (Fulton 2010). Examples of hybrid E2EMs under on-going development include: Spatial Ecosystem And POpulation DYnamics Models (SEAPODYM) (Lehodey et al. 2008) or Object-oriented Simulator of Marine ecoSystem Exploitation (OSMOSE) (Travers-Trolet et al. 2014).

1.3.3. Ecopath with Ecosim

Ecopath with Ecosim (EwE) is commonly described as an ecosystem model, and more precisely corresponds to a quantitative, process-based and species-based model, representing trophic flows in the ecosystem. The EwE modeling approach was primarily developed as a toolbox to help fisheries management and answer 'what if' questions about policy that could not be addressed with single-species assessment models (Pauly et al. 2000, Christensen and Walters 2004, Christensen and Walters 2011). In fact, EwE has been widely applied to inform ecosystem-based management (e.g., Jarre-Teichmann 1998, Plagányi and Butterworth 2004, Christensen and Walters 2011, Coll and Libralato 2012). Also, the EwE software is user-friendly, free (under the terms of the General Public License) and downloadable (www.ecopath.org). Thus, EwE has been applied to hundreds of ecosystems worldwide.

EwE is based on the ECOPATH model, proposed and applied to estimate the main predator-prey pathways in the marine ecosystem of Northwestern Hawaiian Islands (Polovina 1984). The original ECOPATH model was then developed further (Christensen and Pauly 1992), and turned into the EwE modeling framework, which can be seen as a tool-box offering a large collection of methods to analyze various ecological phenomena (Pauly et al. 2000). EwE consists of a suite of three sub-models: (i) Ecopath, static and descriptive; (ii) Ecosim, dynamic and predictive; and (iii) Ecospace, spatially explicit, dynamic and predictive (Christensen and Walters 2004). Ecopath is a descriptive model, representing a static snapshot of the food-web structure, and used as a parameter estimation methodology in the EwE modeling complex (Walters et al. 1997). Ecosim uses the outputs of Ecopath to produce time-dynamic simulations of changing trophic interactions with changes in the ecosystem due to anthropogenic or environmental disturbances (Walters et al. 1997). Ecosim may be used to fit model predictions to time-series data, and to explore alternative fisheries management or climate change scenarios (Christensen and Walters 2004). Ecospace replicates outputs of Ecosim over a spatial grid to explicitly account for the spatial aspects of trophic structure, and was primarily designed for exploring the possible consequences of alternative marine protected areas policies (Walters et al. 1999). Several modules were also developed and added to the EwE package, such as the 'Network Analysis' plugin, a tool available with the Ecopath model (Christensen et al. 2008). The Network Analysis is based on concepts from theoretical ecology, and notably network analysis theory (Ulanowicz 1986, Ulanowicz and Norden 1990, Ulanowicz and Puccia 1990, Ulanowicz 1995).

Ecopath describes the feeding relationships between all species occurring in the modeled food web. Species are aggregated into functional (or trophic) groups, corresponding to an age/size class of a single species, a single species, or a group of species sharing similar ecological traits (such as size, diet, predators, habitat and life cycle), and thus assumed to play similar functional roles in the food web (Christensen et al. 2008). Using functional groups is required to handle diet composition parameters, and also to run the spatially explicit Ecospace model. The main assumption in Ecopath is of mass balance over a given time period (typically one year) (Christensen and Walters 2004). For each functional group, Ecopath assumes that the energy input and output are balanced in the ecosystem, and that the system has the same biomass state at the end of the period as it had at the beginning (Walters et al. 1997). The mass-balance constraint serves as a filter for mutually incompatible estimates in the model. All available information collected about the components of the ecosystem pass through the 'mass-balance filter', which determines what parameters must be to support the current trophic structure and be consistent with observations (Walters et al. 1997, Christensen and Walters 2004).

The parameterization in Ecopath is based on two master equations (Equation 1.1 and Equation 1.2), to which the mass-balance constraint is applied (Christensen and Walters 2004). The first master equation describes the energy balance for each group, so that:

consumption = production + respiration + unassimilated food Equation 1.1

In the second master equation, describing the conservation of biomass, production is split in five components: the biomass removed by natural causes of mortality other than predation (diseases, old age...), by predation, and by fishing, plus the net migration and biomass accumulation:

$$P_i = M_{0i} \times B_i + M_{2i} \times B_i + F_i \times B_i + E_i + BA_i$$
 Equation 1.2

Where, for each functional group *i*, *P* is the production rate $(t \cdot km^{-2} \cdot year^{-1})$, *B* the biomass $(t \cdot km^{-2})$, M_0 the other mortality rate $(year^{-1})$, M_2 the predation mortality rate $(year^{-1})$, *F* the fishing mortality rate $(year^{-1})$, *E* the net migration rate (emigration – immigration) $(t \cdot km^{-2} \cdot year^{-1})$ and *BA* the biomass accumulation rate $(t \cdot km^{-2} \cdot year^{-1})$.

 M_0 , the catch-all rate including all mortalities not elsewhere included, may be expressed through the ecotrophic efficiency (*EE*, dimensionless), which is defined as the part of *P* not directed to detritus, but used by the trophic chain, exported, accumulated or fished:

$$M_{0i} = \frac{P_i \times (1 - EE_i)}{B_i}$$
 Equation 1.3

 M_2 , the mortality rate caused by predation, may be expressed as the sum, over all the predator groups *j* which feed partly on the group *i*, of the product of the consumption/biomass ratios $(Q/B, \text{year}^{-1})$, the biomasses (B_j) and the diet compositions (DC_j) :

$$M_{2i} = \frac{\sum_{j=0}^{n} (Q/B)_{j} \times B_{j} \times DC_{ji}}{B_{i}}$$
Equation 1.4

Therefore, the first master equation may also be written, for each functional group *i*:

$$(P/B)_i \times B_i = (P/B)_i \times B_i \times (1 - EE_i) + \sum_{j=1}^{n} (Q/B)_j \times B_j \times DC_{ji} + Y_i + E_i + BA_i$$

Equation 1.5

Where, for each functional group *i*, *P* is expressed as the product of the production/biomass ratio $(P/B, \text{ year}^{-1})$ and B_i ; and the catch rate $(Y, \text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1})$ is the product of *F* and *B*, and corresponds to the total of all extractions by all the fishing fleets defined in the modeled ecosystem (if exploited).

To estimate the missing parameters, Ecopath solves a system of linear equations (with as many equations as there are groups in the model) by using a generalized method for matrix inversion (Christensen and Walters 2004). For each group, one of the six main parameters (biomass, production/biomass ratio, consumption/biomass ratio, ecotrophic efficiency, net migration rate and biomass accumulation rate) is estimated (ideally the *EE*), and the others must be entered, along with the two remaining ones (diet compositions and catch rates) (Christensen and Walters 2004). Ecopath provides a snapshot of the trophic web consisting of 'instantaneous' estimates of biomasses, trophic flows, and mortality rates, for the reference year or time period (Christensen and Walters 2004).

1.3.4. EcoBase

Building an EwE model requires 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 (Christensen et al. 2008). Then, EwE models help understanding the structure and functioning of the modeled ecosystems, by summarizing all available knowledge on the ecosystems and deriving various system properties (Walters et al. 1997). Thus, EwE-based studies may be seen as important sources of information, and several meta-analyses, based on a selection of EwE models, have been performed (Colléter et al. 2013b). Some meta-analyses studied ecological and trophic concepts (e.g., Christensen and Pauly 1993a, Christensen 1995a, Libralato et al. 2006, Gascuel et al. 2008, Arreguín-Sánchez 2011), while others focused on ecosystems and species of particular interest (e.g., Christensen et al. 2003b, Pauly et al. 2009).

However, only few meta-analyses have been using large collections (more than 50) of EwE models (e.g., Coll et al. 2012, Pikitch et al. 2012, Heymans et al. 2014). These metaanalyses were based on individual datasets since no comprehensive, open-access and digital collection of EwE models was available. Indeed, contrary to other historical "big" sciences, such as oceanography, meteorology or astronomy, extensive data-sharing is not the norm in life sciences, such as ecology, and faces sociological and technological challenges (Pauly 1995, Reichman et al. 2011, Thessen and Patterson 2011). Nevertheless, ecology is following the same path and becoming 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 preexisting large datasets and allowing for new insights on complex or underlying phenomena on global scale (e.g., Christensen et al. 2009). Thus, new practices are needed to make data sharing fully part of the culture in ecology (Zeller et al. 2005, Dalgleish et al. 2012, Hampton et al. 2013). Notably, open-access and digital repositories that "provide standardization, atomization and quality control services facilitate the [discovery, storage and] reuse of data and will play a stronger role in data-intensive science" (Thessen and Patterson 2011).

The EcoBase project was initiated to support and stimulate data sharing and global metaanalyses, using the EwE modeling approach. 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. 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 provide open-access and digital information on the referenced models; (iii) enable global meta-analyses based on EwE models. The EcoBase repository may be accessed online (sirs.agrocampus-ouest.fr/EcoBase/) via different (more or less restrictive) user types and details on the structure, usage, and capabilities of EcoBase can be found in the report introducing it and available online (Colléter et al. 2013b). In the long term, EcoBase is meant to be used by ecosystem modelers worldwide as a platform where to (i) look for published EwE models; (ii) select and access models of interest to their research work; (iii) download models as well as upload their own models.

1.4. Research questions and objectives

The main objectives of this thesis are to propose new methods and provide new insights for understanding, modeling and potentially predicting marine species trophic interactions (MSTI). More precisely, I tackle the following research questions:

- How modeling approaches, such as EwE, are used to model MSTI? What are the potentials and challenges of using the EcoBase information repository to help answering this question?
- Why are MSTI important for the structure and functioning of marine ecosystems?
- Can modeling approaches, such as EwE, help identifying important MSTI? How are MSTI impacted by anthropogenic drivers, such as fishing?
- Can we predict MSTI? What are the potentials and challenges of using the FishBase information repository to help answering this question?

The thesis is structured into six chapters, including the Introduction and Conclusion chapters. In the Introduction, I presented current knowledge on the status, trends, and drivers of changes in the oceans. Loss of biodiversity, and notably loss of trophic diversity due to fishing, was identified as an important driver of changes in marine ecosystems. Concepts and definitions

related to biodiversity, trophic interactions and diet composition were briefly introduced, in a marine context. Then, I introduced the Ecopath with Ecosim (EwE) ecosystem modeling approach, within the framework of Ecosystem Based Management (EBM), and by comparison with other types of models. I also introduced the EcoBase repository of published EwE models worldwide.

In Chapter 2, we use EcoBase to propose a global overview of the applications of the EwE modeling approach. For the 433 unique models documented in EcoBase, we compile, standardize, and analyze all available metadata on the general characteristics of the modeled ecosystems, the objectives, complexity and scope of the models, as well as the associated publication(s). Based on the year of publication of the models, we also analyze the evolution of the EwE applications over the last thirty years. Thus, we intend to provide new insights on the interest for and usage of one of the most widely applied approaches in ecosystem modeling. Moreover, the standardized metadata provided in Chapter 2 are reused as selection criteria to perform a meta-analysis based on EwE models in Chapter 4. Indeed, by applying a scoring method on these criteria, a list of Ecopath models of potential interest is obtained.

Both Chapters 3 and 4 focus on understanding the importance of trophic interactions, using the EwE modeling approach. I briefly mentioned in the introduction different types of species that are critical to the ecosystem, due to their trophic roles. In Chapter 3, I propose a comparative and conceptual framework describing the different categories of critical species, as well as other species of potential managerial interest. I focus on the over-used and much debated concept of keystone species and I intend to clearly defining what is and is not a keystone species. I present a thorough literature review and analyze the origin and evolution of the multiple definitions, terms, and examples associated with the (sometimes inappropriate) applications of the concept in the peer-reviewed literature. Chapter 3 intends to be a proposal for a restored, restrictive and criteria-based definition of the concept of keystone species.

In Chapter 4, I apply the restored definition proposed in Chapter 3 to identify potential keystone species in marine food webs. I perform a meta-analysis, based on 101 published Ecopath models, selected from EcoBase so as to be representative of the variety of marine ecosystems worldwide. Based on the meta-analysis, I derive a functional index of keystoneness (KS) from the EwE modeling approach, directly applicable to marine food webs. Thus, I intend to make the concept of keystone species operational for marine biodiversity conservation. The

proposed KS index is calculated based on estimates of the trophic impact of species in the food web, itself obtained from estimates of the species diet composition (DC). Thus, DC is a critical parameter when assessing the relative importance of species in the food web, based on their trophic interactions. However, as mentioned in the Introduction, DC is one of the least addressed parameter in quantitative trophic flow models, and several factors may prey selection and utilization, notably for fish species.

In Chapter 5, I analyze fish diet composition and intend to identify good predictors of fish feeding selectivity. Multiple approaches have been proposed in the literature to predict fish diet composition, with more or less success. I choose to tackle this issue by using one of the most important open-access, digital and cross-disciplinary information repositories on marine biodiversity: FishBase (www.fishbase.org). I select and extract diet data and a suite of biological and ecological parameters from FishBase for a defined pool of predator and prey species. Predator species are then discriminated based on their diets, and parameters of potential significance to predict predator types are identified.

Finally, I summarize the major results and main conclusions from each chapter in the Conclusion. For each chapter, I also emphasize the applications of the proposed methodologies and the implications of the findings, draw some recommendations, discuss the limitations of the analyses and propose possible perspectives for future improvements.
2. Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase information repository

2.1. 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 on global scale (e.g., Christensen et al. 2009). A popular example of open-access, digital and cross-disciplinary database 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 (Pauly 1995, Edwards 2010, Hampton et al. 2013). Although incentives for digitization of non-digital materials have been growing, existing information repositories, such as FishBase, 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). Yet, 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 (Vision 2010, Thessen and Patterson 2011). Data sharing is not a tradition in ecology and faces multiple sociological and technological obstacles (Reichman et al. 2011, Thessen and Patterson 2011). New practices are needed to make data sharing fully part of the culture in Life Sciences (Pauly 1988, Reichman et al. 2011, Thessen and Patterson 2011, Dalgleish et al. 2012, Hampton et al. 2013). 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 (Vision 2010, Thessen and Patterson 2011). The actual data are meant to be provided in online supplements or upon individual requests sent to the authors, but these options often remain unreliable (Vision 2010). 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).

While facing the challenges related to open-access data, ecology is more and more relying on modeling-based approaches to inform management. In aquatic ecology, the Ecopath with Ecosim (EwE) modeling approach has been widely applied to inform ecosystem-based management (e.g., Jarre-Teichmann 1998, Plagányi and Butterworth 2004, Christensen and Walters 2011, Coll and Libralato 2012), 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 (Pauly et al. 2000, Christensen and Walters 2004, Christensen and Walters 2011). Details on the core principles and equations of EwE can be found 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.

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 (Christensen et al. 2008). By summarizing all available knowledge on the modeled ecosystems and deriving various system properties, EwE models help understanding the structure and functioning of ecosystems (Walters et al. 1997). Thus, EwE-based studies may be seen as important sources of information. On top of detailed information on the modeled ecosystem, which represents essential information to reuse the model for performing meta-analyses. Several meta-analyses, based on a selection of EwE models, have been performed, focusing either on ecological and trophic concepts (e.g.,

Christensen and Pauly 1993a, Christensen 1995a, Gascuel et al. 2008, Arreguín-Sánchez 2011), or on ecosystems and species of particular interest (e.g., Christensen et al. 2003a, Christensen et al. 2003b, Libralato et al. 2006, Pauly et al. 2009). However, only few meta-analyses have been using large collections of EwE models (more than 50) (e.g., Coll et al. 2012, Pikitch et al. 2012, Heymans et al. 2014). These meta-analyses were based on individual datasets since no comprehensive, open-access, and digital collection of EwE models was available, and this is why EcoBase was created.

The EcoBase project was initiated to support and stimulate data sharing and global metaanalyses using the EwE modeling approach. 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. The EcoBase repository may be accessed online (sirs.agrocampus-ouest.fr/EcoBase/) via different (more or less restrictive) user types and details on the structure, usage, and capabilities of EcoBase can be found in the report introducing it and 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) enable global meta-analyses based on EwE models. In the long term, EcoBase is meant to be used by modelers as a platform where to (i) look for published EwE models; (ii) select and access models of interest to their research work; (iii) download others' models as well as upload their own models.

In this study, we used EcoBase to compile available critical metadata on all the EwE models referenced in the models repository. We analyzed the metadata to propose a global overview of the applications of the EwE modeling approach in the scientific literature. We focused 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). We first presented a general description of the EwE applications published worldwide. Based on the year of publication of the models, we then analyzed the evolution of the EwE applications over the last three decades. We also analyzed the contribution of EwE-based studies in the scientific literature. We intended to provide new insights on past and recent usage of and interest for the EwE modeling approach in the scientific community.

2.2. Methods

2.2.1. Compilation of the models and publications

2.2.1.1 Compilation of 433 EwE models

In EcoBase, we completed an inventory of all EwE models published from 1984 to 2014 (Colléter et al. 2013b). Our 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). The EwE modeling approach and software consists of a suite of three sub-models (or routines): (i) Ecopath, a static and descriptive model, representing a mass-balanced snapshot of the food web; (ii) Ecosim, a dynamic and predictive model, producing time-dynamic simulations for exploring alternative scenarios, based on Ecopath; and (iii) Ecospace, a spatially-explicit version of Ecosim (Christensen and Pauly 1992, Walters et al. 1997, Walters et al. 1999, Christensen and Walters 2004). 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 (Colléter et al. 2013b), some duplicates were first obtained and we then extracted a list of 433 'unique' EwE models from the 571 models recorded in EcoBase. Unique models were defined by the ecosystem they represented (i.e. the model area), the time period they covered (i.e. the model start and end years), and the author of the model (i.e. the first author on the reference of the model, commonly considered as the modeler who developed the model). Thus, if several models represented the same ecosystem but, either over older or more recent time periods, or over smaller or larger areas, or were developed by different modelers, then they were considered as unique. In addition, models representing the same ecosystem over different time periods were specifically identified as 'replicates'. Most of the time, replicates were built by the same author and comprised the same number of groups, although there were some exceptions. The analyses presented in this study are based on the 433 unique EwE models documented in EcoBase (see

Appendix A and the EcoBase website for detailed references of the models). For each of the 433 models, we compiled, standardized and encoded in EcoBase all available metadata.

2.2.1.2 Compilation of 397 EwE-base publications

In parallel, we conducted a comprehensive literature review and compiled 397 publications presenting EwE-based studies. 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. We considered five publication types: journal articles, reports (entire report and report sections), book sections, theses, and conference papers. For journal articles, we also analyzed the number of publications by scientific journal, based on the title of the journals. Each of the 433 EwE models was associated to its corresponding publications. One model could have been described in more than one publication. In that case, we classified the publications 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. When several references were available for one model, the primary one was used to define the year of publication. In the end, each model was associated to at least one (primary) reference. Then, the models were aggregated, based on their year of publication, into three groups corresponding to the last three decades (1984-1993; 1994-2003; 2004-2014), so as to analyze the evolution of EwE applications over time. Note that the same publication could describe several EwE models, so that we obtained only 397 publications for 433 models.

2.2.2. Compilation of the metadata

For each of the 433 models, we analyzed the metadata describing: (i) the characteristics of the modeled ecosystems; (ii) the research objectives of the modeling approach; and (iii) the structure, scales and units of the models (see Table 2.1 for the detailed list of metadata). All data used in this study may be downloaded on the EcoBase website.

2.2.2.1 Characterization of the modeled ecosystems

The 433 models were classified based on the characteristics of the ecosystems they represented and using information provided in the associated publications. First, using expert knowledge, we defined 13 ecosystem types: bay/fjord, beach, channel/strait, coastal lagoon, continental shelf (down to 200 m depth), coral reef, estuary, lake, ocean (deeper than 200 m), reservoir, river, terrestrial, and upwelling. 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, we documented the geographic extent of the models, 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. When no precise indication was given, the spatial shape was defined as a point. The centroid of the spatial shape defined for each model was used to determine the climatic zone of the model. Three climatic zones were defined based on latitude: tropical-subtropical (less than 30°N/30°S), temperate (greater than or equal to 30°N-58°N/30°S-58°S), and high latitude (greater than 58°N/58°S) (Pikitch et al. 2012). 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 365 models representing marine ecosystems were classified into FAO areas, while the subset of 345 models representing coastal marine ecosystems was classified into LMEs.

2.2.2.2 Identification of the research objectives of the modeling approach

We classified the research objectives of the 433 EwE models into seven topics, i.e., (1) aquaculture; (2) ecosystem structure and functioning; (3) environmental variability and climate change; (4) fisheries; (5) Marine Protected Areas (MPA); (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. Although the 433 EwE models were defined based on the implementation of the Ecopath routine, we compiled metadata indicating if the Ecosim or Ecospace routines had also been used. Ecosim and Ecospace models add complexity to the Ecopath base models and enable to explore alternative management scenarios by representing the temporal and spatial variability of the ecosystem.

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, we considered three plug-ins of potential interest: Ecotracer, EcoTroph, and Keystoneness. Ecotracer uses Ecosim to predict movement and accumulation of contaminants and tracers in food webs (Coombs 2004, Booth and Zeller 2005). 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, 2008). EcoTroph is based on synthetic representation of ecosystems using trophic spectra, i.e. the continuous distribution of biomass (or production, catch, fishing mortality) as a function of continuous trophic levels (Gascuel and Pauly 2009, Gascuel et al. 2011). It enables the simulation of various fisheries changes and their impacts on computed trophic spectra, and provides indicators of the ecosystem impacts of fishing (Tremblay-Boyer et al. 2011, Colléter et al. 2013a, Gasche and Gascuel 2013). 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).

2.2.2.3 Description of the structure, scales and units of the models

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 433 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, and may be used for a species with a complex trophic ontogeny. Thus, species defined using multi-stanza groups add levels of complexity in the models.

When specified in the associated publications, the temporal and spatial scales of the 433 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, we compiled as first and last years, the records of the start and end years of the modeled periods, as stated by the modelers in the publications. 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 area (in km²) covered by the EwE models was also documented. Lastly, currency and time units of the models were documented.

2.3. **Results**

2.3.1. General description of the EwE applications published worldwide

Globally, EwE models have been mainly developed to study marine ecosystems in the tropical or temperate zones, with some regions better covered than others. 84% of the models (i.e. 365 models) represent marine ecosystems, whereas 15% (63 models) represent freshwater ecosystems and 1% (5 models) terrestrial ones (Figure 2.1a). 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 (Figure 2.1b). 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 2.1c).

Four LMEs did not comprise any EwE models: the Somali Coastal Current, the Oyashio Current, the East Siberian Sea, and the Laptev Sea. Overall, the Northern and Central Atlantic Ocean is the region with the highest proportion of EwE models, whereas fewer EwE models have been developed for the Indian and Antarctic Oceans. 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 2.2a). In the freshwater category, lake is the top represented ecosystem type, with 8% of the models. Based on the climatic zone we defined, 49% of the models are located in the tropics, while 44% are located in temperate areas and only 7% in high latitudes.

EwE models were used to tackle a wide range of ecological issues (Figure 2.2b). 87% of the models were developed to answer questions regarding the structure and functioning of the ecosystem, 64% to analyze fisheries, 35% to focus on particular species of interest, and 11% to consider environmental variability. Less than 10% of the models tackled issues related to MPA, pollution or aquaculture. Time dynamic simulations in Ecosim were performed for 41% of the models, and spatially-explicit versions were developed in Ecospace for 7% of the models. The Keystoneness tool has been used in 11% of the EwE models (47 models). The EcoTroph and Ecotracer plug-ins have been rarely applied (i.e., in 2% and less than 1% of the models, respectively).

Overall, the majority of the models represented ecosystems between 1980 and 2009, over a time period of one year and an area ranging from 10,000 to 1,000,000 km², and comprised from 10 to 40 functional groups. About two thirds of the 433 EwE models comprise between 10 and 40 functional groups, with 33% (141 models) including 10 to 20 groups (Figure 2.2c). 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, 30% of the models comprise groups corresponding to stanzas. About two third of the models refer to a time period comprised between 1980 and 2009, with 37% (159 models) corresponding to the 1990s (Figure 2.2d). Of the 433 unique models, about 30% (132 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. About two thirds of the models cover a time period lasting from one to five years, with 44% (191 models) corresponding to one year, which is the classical temporal scale of Ecopath models (Figure 2.2e). The longest time period represented by a model is 40 years. The spatial extent covered by the models varies widely, from 0.005 km² to 34,640,000 km² (Figure 2.2f). Though, model area does not exceed 1,000,000 km² for most models, and half of the models cover an area ranging from 10,000 to 1,000,000 km². Twenty-two models were developed without specifying any temporal scale and 75 models without indicating any spatial scale. Finally, 89% of the 433 EwE models use wet weight as currency unit (of which 88% express it in t·km²), 5% carbon, and 4% dry weight. Only three models use calories, one model joule and one model nitrogen. Almost all models use year as time unit, while only ten models use day, month, or season.

The 397 EwE-based studies were mainly published in the peer-reviewed literature, with 213 research articles published in 60 different scientific journals. However, only a few of the journals published more than three articles (Table 2.2). *Ecological Modelling* published the highest number of EwE-based studies (76 articles, i.e. 36%), followed by *Estuarine, Coastal and Shelf Science* (6%), and *Progress in Oceanography* (5%).

2.3.2. Evolution of the EwE applications over the last three decades

Over the last three decades, EwE applications have progressively been developed in all regions of the world's oceans. 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 (Figure 2.3a). 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 (Figure 2.3b). 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 (Figure 2.3c).

During the first decade of its development (1984-1993), the EwE modeling approach essentially consisted of Ecopath models representing tropical marine systems and using a simple trophic structure. In contrast, during the last two decades (1994-2014), EwE models were applied to a wider variety of ecosystems, including high latitudes and terrestrial systems. Besides, the numbers of models representing freshwater ecosystems has doubled over the last two decades (Figure 2.4a). 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 2.4b). Since 1994, the proportions of both tropical and temperate systems have stabilized between 40 to 50%. From 1994 to 2014, 32 models representing ecosystems at high latitudes have been published.

EwE models were also progressively used to answer a wider range of research questions, such as issues related to pollution or aquaculture (Figure 2.4c). 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 10% in 1984-1993 to 30% in 1994-2003). The number of models built to study environmental variability (including climate change) and MPAs, respectively, has gradually increased since 1984, although their respective proportions have remained lower than 10%. The proportion of models focusing on a particular species (or taxa) of interest has stayed more or less constant over time (at about 15%).

Over the last 30 years, modeling practices have evolved toward Ecopath models with more complex trophic structure, shorter temporal scales, and larger spatial scales. 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 (Figure 2.4d). Over time, the range of the number of groups has expanded toward more groups, up to 67 groups in the last decade (excluding the few outlier models). Besides, the median is around 15 groups in 1984-1993, while it is around 30 groups in 2004-2014. Thus, recently developed models tend to be less aggregated and thus more complex, although highly aggregated models are still being proposed in recent times.

In contrast, the time period represented by the models tends to decrease over the last 30 years (Figure 2.4e). 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. Besides, the proportion of models corresponding to replicates of the same ecosystem over different (anterior or posterior) time periods has been increasing through time: from 24% of replicates published in 1984-1993, to 27% in 1994-2003, and 33% in 2004-2014. The areas covered by the models have always varied over a wide range (Figure 2.4f). Nevertheless, in the last two decades, the range of the models area has expanded toward very

large areas, and the median has shifted accordingly, from about $1,000 \text{ km}^2$ in 1984-1993 to about 100,000 km² in 1994-2014.

Over the last 30 years, the numbers of EwE-based publications has steadily increased (Figure 2.5). The annual number of publications 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. Thus, of the 397 EwE-based studies published over the last three decades, 9% were published in 1984-1993, 29% in 1994-2003, and 62% in 2004-2014 (respectively 35, 114, and 248 publications). Likewise, the cumulated number of EwE users (first authors on publications) has significantly increased over time, from 30 users in 1993, to 98 in 2003, and 230 in 2014 (Figure 2.5). Moreover, both the number and proportion of peer-reviewed publications presenting EwE applications have been growing over the last three decades (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.

2.4. Discussion

2.4.1. Challenges and potentials of the compilation and meta-analysis of EwE models

All the metadata analyzed in this study were collected or derived from the publications presenting the EwE models. However, detailed information on some metadata was sometimes missing for many models, which prevented us from using the whole collection of metadata initially envisaged. Lack of information was sometimes observed for metadata of potentially high relevance to the EwE modeling approach. For instance, we obtained 5% of missing data regarding the time period represented by the models, and 17% for the area covered by the models. Though, it is critical to clearly define and indicate the temporal and spatial scales when

developing a model. When the geographic extent of the models was poorly described, no spatial shape could be defined for these models. Likewise, several metadata describing the physical characteristics of the modeled ecosystems were considered in EcoBase (e.g., temperature, depth, salinity, oxygen, primary production), but information on abiotic conditions was lacking for most models. Remarkably, information on minimum and maximum depths of the area covered by the models, which is critical to determine the type of ecosystem represented by the models, was sometimes not provided in sufficient details. Moreover, the compilation of the metadata was sometimes challenging due to some ambiguity in the description of the model. Some models included functional groups labeled as stanzas, but which were not always properly defined as multi-stanzas groups. Thus, we were not able to analyze in many details the usage of multi-stanzas groups.

For some metadata, the proportion of models with non-available information was too high for the metadata to be representative. 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, we intended to analyze the evolution of the use of the different versions. 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, Christensen and Pauly 1992) rapidly led to a broader use of the model. Versions 3 and 4 only had limited use and were rapidly replaced by version 5 (Christensen et al. 2005), which is now itself replaced by version 6 (Christensen et al. 2008). However, the EwE software versions were only specified by modelers for half of the models, so that we could not explore this aspect of the modeling approach much further. Likewise, the Pedigree index, corresponding to an estimation of the data quality of the models (Pauly et al. 2000), could not be analyzed since it was provided for only very few models.

The challenges we faced during the collection and compilation of the metadata emphasized the need for defining and enforcing best modeling practices (FAO 2008). Precisely, we would strongly recommend EwE modelers to provide basic information about their models in sufficient details in the associated publication(s). As a template, we would suggest the following metadata to be considered as essential: location, objectives, area, time period, units, software version, Pedigree index, trophic structure, and environmental conditions. Requiring such information to be systematically provided would facilitate the reuse of the models, and thus

increase the scientific value of EwE-based publications. Indeed, the metadata compiled in this study could serve as valuable criteria based on which EwE models would be selected for future studies. By applying a scoring method on these selection criteria, a pool of models of potential interest would be defined and the selected models could then be reused to perform EwE-based meta-analyses. Thus, EcoBase offers a framework where the metadata could be stored, in a standardized and granular fashion, so that they could be easily reused.

2.4.2. Conclusions on the EwE modeling approach: past, present and future

The metadata compiled for this study were used to give a global overview of the EwE models and EwE-based publications. We also analyzed the evolution of the EwE applications over time, based on the year of publication of the models. 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 (Christensen and Pauly 1993b). EwE was also early applied to freshwater ecosystems, likely due to the ease for defining the boundaries and components of systems such as lakes or rivers. Over the last three decades, some regions have been widely analyzed using the EwE modeling approach, while others have remained poorly-studied. The focus of EwE applications on some regions, such as the North and Central Atlantic Ocean, were driven by research programs and funding opportunities, but also by data availability. In contrast, future modeling efforts could be concentrated in the Indian and Antarctic Oceans, seeing the smaller number of applications in these regions. Terrestrial systems have been very poorly studied using EwE until now. However, interests have recently been growing for applying the EwE modeling approach to terrestrial case studies (Fretzer 2014).

Over the last three decades, the research questions addressed using EwE models have progressively become more diversified. Particularly, the usefulness of EwE models for fisheries management has been demonstrated in several cases, such as upwelling systems (Jarre-Teichmann 1998) or the Mediterranean Sea (Coll and Libralato 2012). More generally, the main strengths of EwE relate to the improved understanding of the trophic structure of the modeled ecosystem and the possible comparison between modeled ecosystems (Jarre-Teichmann 1998,

Plagányi and Butterworth 2004). In parallel, the complexity of the EwE models has been increasing, notably with the inclusion of more functional groups and the evolution toward a partitioning approach for the representation the food web in some cases. However, a significant proportion of recent EwE applications focused on some species (or taxa) of particular interest, so that the representation of the food web was centered on these species, using a more selective approach.

Despite the development of the Ecosim routine allowing for time-dynamic simulations (Walters et al. 1997, Walters et al. 2000, Walters et al. 2006, Walters and Christensen 2007), the static Ecopath routine has also been used to analyze changes in ecosystems over time, through the comparison of replicate models. Indeed, using replicates of Ecopath models may constitute an easier (and complementary) approach than performing simulations in Ecosim, which are more complex and data-demanding. Despite its complementarity with Ecosim, the Ecospace routine has been little used to date (7%). In fact, Ecospace has been proposed more recently (Walters et al. 1999) and the latest improvements made to the routine have not been widely disseminated yet (Walters et al. 2010, Christensen et al. 2014b). Likewise, EcoTroph is a relatively recent plug-in (Gascuel and Pauly 2009), which has thus been rarely applied, but the recent implementation of the plug-in in R (Colléter et al. 2013a) may allow for a wider application. With the release of EwE version 6, more flexibility was implemented in the software and users were given access to the source code of the model. Thus, EwE modelers will be more and more inclined to develop their own plug-ins (e.g., Coll and Steenbeek 2014) and take full advantage of the multiple potentials of the EwE modeling approach, including the EcoBase repository.

Metadata	EcoBase field	Definition	
Aquaculture	aquaculture	Was the model developed to analyze aquaculture? (TRUE/FALSE)	
Area	area	Model area (in km ²)	
Climatic zone	classification	Climatic zone of the modeled ecosystem	
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 category	ecosystem_category	Category of the modeled ecosystem	
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 climate variability? (TRUE/FALSE)	
First Year	model_year_start	Start year of the model time period	
Fisheries	fisheries	Was the model developed to analyze fisheries? (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)	
Last Year	model_year_end	End year of the model time period	
Model	model_number	Model number (3-digits code) as recorded in EcoBase	
MPA	mpa	Is the modeled ecosystem a Marine Protected Area? (TRUE/FALSE)	
Number of groups	number_groups	Number of functional groups included in the model	
Pollution	pollution	Was the model developed to analyze pollution? (TRUE/FALSE)	
Publication	id_ref	Publication number (3-digits code) as recorded in EcoBase	
Publication	xml_ref	Reference in xml format (including author, year of publication, and type of publication)	
Reference	referenced	Is the reference of the model recorded in EcoBase? (TRUE/FALSE)	
Reference	ref_importance	Importance of the reference (1 by default)	
Replicates		Model number(s) of the replicate(s)	
Replicates	overlapping_model	Are there other models representing the same ecosystem	
Species	species_of_interest	Was the model developed to study a particular species/group? (TRUE/FALSE)	
Stanzas	stanza_groups	Are there any stanzas in the model? (TRUE/FALSE)	
Time unit	time_units	Time unit of the model	
Version	ewe_version_original	Version of EwE used by the modeler	

Table 2.1. List of the metadata used for the analyses. Metadata are listed in alphabetical order, with their corresponding fields in EcoBase and definitions.

Journal	Number of articles	Percentage
Ecological Modelling	76	36
Estuarine, Coastal and Shelf Science	12	6
Progress in Oceanography	10	5
Journal of Marine Systems	9	4
Marine Ecology Progress Series	9	4
Canadian Journal of Fisheries and Aquatic Sciences	8	4
African Journal of Marine Science	5	2
Bulletin of Marine Science	5	2
Fisheries Research	5	2
ICES Journal of Marine Science	4	2
Journal of Experimental Marine Biology and Ecology	4	2
Others	66	31

Table 2.2. Number and percentage of articles presenting EwE-based studies, detailed by journal.



Figure 2.1. 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 365 models representing marine ecosystems are represented on the FAO area map, and the 345 models representing coastal marine ecosystems on the LME map.



Figure 2.2. Classification of the 433 unique EwE models documented in EcoBase by: (a) type of ecosystem represented by the models; (b) research questions answered with the models; (c) number of functional groups of the models; (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 x-axis, and in number on the top of each bar. Missing data are displayed as 'NA' for Non Available.



1994 - 2003





Figure 2.3. World maps of the number of EwE models documented in EcoBase by FAO area, for each of the last three decades: (a) 1984-1993; (b) 1994-2003; and (c) 2004-2014.



Figure 2.4. Comparison of the classified EwE models between the last three decades: 1984-1993; 1994-2003; and 2004-2014; based on the year of publication of the models. Classification of the models by: (a) category of ecosystem represented by the models; (b) climatic zone of the modeled ecosystems; (c) research questions answered with the models; (d) number of functional groups of the models; (e); time period (in number of years) represented by the models; and (f) area (in km²) covered by the models. On the bar plots, values are displayed in percentage on the y-axis, and in number on the top of each bar. On the boxplots, the horizontal line in the box represents the median number of models.



Figure 2.5. Number of publications presenting EwE-based studies over the last thirty years. For each decade (1984-1993, 1994-2003, and 2004-2014), a pie chart shows the repartition of the publications by type. The two vertical dotted lines highlight the transition years between the three decades. The black solid line represents the number of all types of scientific publications while the gray solid line represents journal articles only. The dotted line represents the cumulated number of first authors associated to the publications from 1984 to 2014.

3. Proposal for a restored definition of the concept of 'keystone species'

3.1. Introduction

The ecological term of 'keystone' species, introduced in aquatic food web ecology by R. T. Paine (1969a, Paine 1969b), is based on the analogy between a natural ecosystem and a stone arch. The keystone refers to the stone that maintains all the others in the arch. Both the species and the stone "derive their functional importance to the system as a whole from bidirectional interactions with lower energy levels" (Davic 2003). If the keystone is removed, the structure of the arch is removed as well, as the remaining stones can only form simpler structures, such as a stack or a wall (Platten and Henfrey 2009). Therefore, in the community, as well as in the stone arch, the keystone species fulfills an irreplaceable function by maintaining its structure (Paine 1969a), and only a limited number of species can be keystone (Power et al. 1996).

Since its introduction, the keystone species concept had been applied to a large number of aquatic and terrestrial species, playing a variety of critical roles in the ecosystem (Paine 1995, Power and Mills 1995, Power et al. 1996). The relevance of such an over-used ecological concept was much debated in the literature (Hurlbert 1997), either described as a powerful buzzword in conservation (Barua 2011), or criticized as an ambiguous and inclusive concept (Cottee-Jones and Whittaker 2012). The concept first appeared to be attractive to managers, looking for species-level regulations in a context of ecosystem-based approaches to conservation (Simberloff 1998). The notion seemed valuable for communicating on the fragility and importance of balances in natural systems (Paine 1995, Piraino et al. 2002). Because of its metaphorical nature, which evokes concrete images, the keystone species term was very popular to both the general public and the scientific community, and helped bridging the gap between scientific knowledge, conservation action, and public awareness (Barua 2011). For instance, 'keystone species' was the most frequently encountered metaphorical ecological concept in English newspapers during an 8-year period starting in 2000 (Barua 2011), and was used in 1,600 scientific articles' title or topic description published by 2012 (Cottee-Jones and

Whittaker 2012). The keystone species concept was seen as a helpful concept for (i) identifying species whose removal would have unsuspected and dramatic consequences on their communities; (ii) understanding the complex underlying mechanisms of community dynamics; and (iii) considering the whole ecosystem functioning and structure to inform biodiversity conservation (Paine 1995, Power et al. 1996, Simberloff 1998). Paine's articles introducing the concept and published in 1966 and 1969 were cited 2,509 and 465 times in the peer-reviewed literature, respectively (Cottee-Jones and Whittaker 2012).

Yet, the wide-spread use of the terminology led to misusages, and semantic confusion with other overlapping concepts was introduced. For instance, the keystone species term was defined in only 35% of the English news articles cited above, with less than half of the articles providing accurate definitions (Barua 2011). Ecosystem engineer species were notably found to be often mislabeled as keystone species (Barua 2011, Cottee-Jones and Whittaker 2012). In fact, the keystone species term (like several other scientific terms) had been promoted by the scientific community, before any consensus on its exact meaning and implications for biodiversity conservation was reached, leading to high misrepresentation (Hurlbert 1997, Barua 2011, Cottee-Jones and Whittaker 2012). Consequently, the keystone species concept rapidly evolved to become what might be called a 'non-concept' (a concept with uncertain meaning), or a 'panchestron' (a concept "which can explain anything and thus nothing at all" (Hardin 1957)) (Hurlbert 1997, Cottee-Jones and Whittaker 2012). As pointed out by Paine (1995), "An answer serving all masters probably provides few useful solutions". Consequently, the keystone species concept was criticized for its lack of clear and operational definition, preventing its implementation for management and policy-making (Mills et al. 1993, Hurlbert 1997). Often, species depicted as keystone gained preference over the ultimate objective of biodiversity conservation (Barua 2011).

In this study, we argued for the restoration of the over-used concept of keystone species. We intended to clearly define what are and are not 'keystone species', and proposed a restored definition of the keystone species concept. To do so, we conducted a thorough literature review and analyzed the origin and evolution of the multiple definitions, terms, and examples associated to the keystone species concept in the peer-reviewed literature. First, we built an evolutionary tree to represent the usages of the concept over time in the scientific literature. Then, we proposed a comparative framework describing the different categories of species of potential

interest, including keystone species. We used our framework to differentiate examples of misusages from appropriate applications of the keystone species terminology in the literature. We concluded by a conceptual diagram representing a restrictive and criteria-based definition of the keystone species concept, which was confronted to related notions in functional ecology and food web theory. Lastly, challenges related to the context-dependency and applicability of the keystone species concept were discussed and illustrated.

3.2. Methods

We conducted a historical review of the peer-reviewed literature on keystone species. Using Google Scholar, we gathered research articles published in scientific journals, from 1966 to 2013, and written in English. We first selected peer-reviewed articles with a clear focus on keystone species (term explicitly mentioned in their title or topic description). We then extended our selection to articles dealing with concepts overlapping with the keystone species concept (e.g., ecosystem engineers). We identified 101 relevant articles on keystone species, with a broad scope and including detailed semantic, practical and/or theoretical considerations. We used the selected articles to analyze the origins and evolution of the keystone species concept. The multiple definitions, terms, and examples of keystone species in marine, freshwater or terrestrial systems, proposed in the 101 articles were collected and synthetized.

First, we used an evolutionary tree to represent the temporal evolution of the semantic usages of the keystone species concept. We summarized on the tree the different terminologies that were introduced over time in the scientific literature. Then, we developed a comparative framework describing the different categories of species of potential interest to conservation and management, including keystone species. For each category, a detailed definition, illustrative examples and references from the literature were compiled, so as to clearly differentiate the concept of keystone species from overlapping concepts.

Keystone species is an ill-defined concept, so that there are many species once labeled as keystone that probably should not be called so (Zacharias and Roff 2001). Thus, we used our framework to differentiate examples of misusages from appropriate applications of the keystone species concept in the literature. Species frequently labeled as 'keystone' in the literature, but not matching all criteria to be *sensu stricto* keystone species, were labeled as 'pseudo-keystone'

species. We determined the categories to which they would rather correspond by comparing the description of their roles in the literature to the definitions compiled in our conceptual framework. We focused on the best-known examples of *sensu stricto* keystone species and the most commonly cited example of pseudo-keystone species. We acknowledged that many more examples could be found in the literature but the ones listed in our review were the most representative ones. Besides, the majority of the examples that could be encountered in the literature would correspond to pseudo-keystone species, because of the increasing misusage of the concept.

Lastly, we identified the required attributes for a species to be defined as keystone species. We looked back at the original definition proposed by Paine (1969b): "The patterns of species occurrence, distribution and density are disproportionately affected by the activities of a single species of high trophic status". Based on the latter definition, we determined the exclusive attributes of keystone species. We used a conceptual diagram to represent the restored definition of the keystone species concept. Our definition includes the four primary web features that were highlighted by Paine (1980): (1) the number of species involved, (2) the nature of their connections, (3) the number of connections per species, and (4) the intensity of connections between species.

In our study, we claimed that the concept of keystone species cannot be dissociated from the notion of species. Therefore, we avoided to use some terms commonly found in the literature, such as 'keystone role' or 'keystone effect', and restricted ourselves to the 'keystone species' or 'keystoneness' (i.e. the potential of a species to be keystone) terminology.

3.3. Results

3.3.1. Evolution of the keystone species concept

We reviewed the evolution of the keystone species term over time in the peer-reviewed literature and summarized it in an evolutionary tree (Figure 3.1).

Paine (1966) first described the underlying mechanisms of the keystoneness of a predator species in rocky intertidal marine communities. The keystone species played the critical role of

maintaining high species diversity and complex trophic structure in the community (Paine 1966). Thus, variations in the keystone species abundance or activity would have greater impacts on the biodiversity and trophic structure, compared to other coexisting species with similar or higher abundance (Paine 1969a, Paine 1969b). Paine's definition emphasized three main criteria for a species to be a keystone species: a single, native, and predator species. Moreover, Paine's definition highlighted two main traits of keystone predator: (i) feeding on a highly competitive prey; and (ii) predating on this prey at all stages of the prey life cycle (Paine 1980).

Since Paine's analogy, the keystone predator concept rapidly expanded to include almost all species playing just about any role in the community, provided that their effects were considered to be significant at the ecosystem scale. After reviewing the usages of the keystone species term in the literature, Mills et al. (1993) proposed a typology comprising several terms describing keystone species, deviating from the original term: 'keystone predator', but also 'keystone prey', 'keystone host' (also called 'keystone resource', such as plants or corals), 'keystone mutualist' or 'keystone link' (e.g., pollinators, seed dispersers), 'keystone modifier' (e.g., beavers building dams, termites building mounds), and 'keystone herbivore' species (e.g., sea urchins). Bond (1994) also proposed a classification of the different types of keystone species discussed in the literature. Some of the types corresponded to the ones previously described ('keystone predators', 'keystone herbivores', 'keystone mutualists' (including 'keystone plant resources'), and 'earth-movers'), while others were newly formulated ('keystone pathogens', 'keystone competitors', and 'abiotic processes') (Bond 1994). The author acknowledged that there was little supporting evidence for some of the terms, which were not explicitly associated to the terminology keystone (e.g., 'dispersers', 'pollinators', or 'system processes'), while the best evidence was for 'keystone predator' (Bond 1994). Both of the latter typologies illustrates that the concept was applied to a variety of species, occupying different trophic levels and having diverse types of interactions within their communities (not only trophic, but also physical interactions through the habitat) (Mills et al. 1993).

The expansion of the keystone species concept was discussed by the "keystone cops", a group of experts who attempted to refine the notion during a workshop in 1994 (Paine 1995, Power and Mills 1995). The experts reached a consensus on the following definition: "a species whose impacts on its community or ecosystem are large, and much larger than would be expected from its abundance" (Power and Mills 1995, Power et al. 1996). Thus, any species

causing disproportionate effects on its community could be considered as a keystone species, including: predators, competitors, mutualists, seeds or spores dispersers, pollinators, producers, parasites, vectors of disease, and modifiers of habitats or abiotic factors (Paine 1995, Power et al. 1996). The workshop participants concluded that a keystone species may occur in all ecosystems, at all trophic levels, and use all kinds of ecological processes (Paine 1995, Power and Mills 1995, Power et al. 1996). Nevertheless, they acknowledged that examples of keystone species with a low trophic level did not meet Paine's original criteria, but were essentially based on the large impact of the species, unexpected from their relatively low abundance (Power et al. 1996).

A keystone species had simply become a species with high functional importance (Hurlbert 1997), and was often equally defined and labeled as a 'key' species (e.g., Khanina 1998, Higdon 2002). Despite the call of some authors against the misinterpretation of Paine's original definition (Piraino and Fanelli 1999, Davic 2000), the keystone species concept was applied to an increasing number of species, based on inclusive (re)definitions. For instance, Menge and Freidenburg (2001) listed all kinds of consumers as potential keystone species (comprising predators, parasites, pathogens, herbivores, pollinators, and mutualists, but not plants), while Davic (2002) argued that the concept could be expanded to any species regulating functional diversity, such as primary producers, fungi and bacteria.

The keystone term was progressively detached from the notion of species. In some cases, 'keystone' was extended to other notions with a broader scope, such as 'keystone guilds' (Brown and Heske 1990), 'keystone habitats' (Davidar et al. 2001), 'keystone structures' (Tews et al. 2004), 'keystone populations' (Perry 2010), 'keystone communities' (Mouquet et al. 2012), or 'keystone species complexes' (Daily et al. 1993, Ortiz et al. 2013b). In other cases, the keystone term was applied at smaller scales, to the extended concepts of 'keystone molecules' (Zimmer and Ferrer 2007) or 'keystone individuals' (ModImeier et al. 2014). Recently, Cottee-Jones and Whittaker (2012) proposed a generic definition: "a keystone species is of demonstrable importance for ecosystem function", where the term 'species' could be replaced with any other ecologically relevant term. Specific traits associated to the historical definition (e.g., single species, disproportional impact and food web structure) were abandoned (Cottee-Jones and Whittaker 2012).

3.3.2. Different categories of critical species, including keystone species

Seeing the ambiguity around the keystone species terminology, a clear discrimination between the concept of keystone species and all overlapping concepts was required. We extricated the keystone species concept of all the other concepts used in the literature to describe species which are of potential interest, yet not necessarily keystone (Table 3.1, Figure 3.2 and Figure 3.3).

First, the concept of keystone species is sometimes assimilated to 'invasive' and 'endangered' species. However, these two terms should be differentiated from the other ecological concept listed below. Often because of human activities, invasive species are introduced to a new ecosystem, where they may cause transient disturbance, until they get established or perish. The ecological role of invaders remains uncertain until they manage to establish themselves in the new ecosystem (Bond 2001). So, the potential effects of invasive species occur beyond the evolutionary time scale of the community (Paine 1980). Moreover, once invaders are established in the new ecosystem, they may become abundant and dominate the species assemblage. Therefore, invaders should not be considered as keystone species in the introduced range. We note that invasive species acting as ecosystem engineers were given a different name in the literature, and called 'transformer species' (Richardson et al. 2000). Thus, invaders acting as keystone species should also be given another name to differentiate them from native species. Endangered species, such as the ones listed on the IUCN Red List (www.iucnredlist.org), are threatened by extinction in their native range, so that their ecological roles may be impaired (Powles et al. 2000). Such species may have played a keystone or another important role in the ecosystem in the past, when they were abundant enough. Yet, due to anthropogenic or environmental threats, they sometimes become 'ecologically extinct' and are not able to fulfill any ecological role anymore (e.g., overhunted sea otters) (Jackson 2008).

3.3.2.1 Focal species *versus* surrogate species

We clearly discriminated two broad categories of species: 'focal species' and 'surrogate species'. Focal species correspond to species which are selected to preferentially focus on, among all species in the community (Armstrong and Caro 2002). Surrogate species designates

species that are substitute for something else (Armstrong and Caro 2002), used as tools to achieve another purpose (Caro and O'Doherty 1999), and considered as "shortcuts" for biodiversity management and conservation (Roberge and Angelstam 2004). Thus, a focal species is assumed to be of importance to its ecosystem, whereas a surrogate species may not be of intrinsic interest (Armstrong and Caro 2002). Both terms were introduced at the same period: focal species was first coined by Lambeck (1997), while surrogate species was first used by Caro and O'Doherty (1999). Although the two terminologies imply different assumptions and objectives, they have often been used very loosely in the literature, sometimes as synonyms (Caro 2010). That is why some authors recommended to "define precisely what we are talking about instead of using insider jargon", such as surrogate or focal species (Armstrong and Caro 2002).

3.3.2.2 Sub-categories of focal species

In this study, we defined critical species as focal species of ecological importance that play an important role for the structure, composition or functioning of its ecosystem, so that the absence of these species would lead the loss of many others. Critical species may also be called 'ecologically important species' (Perry 2010). Critical species had been compared, and sometimes assimilated, to critical processes (e.g., Bond 1994), since some critical processes may be driven by critical species (Power et al. 1996). Yet, the biotic and abiotic factors influencing ecosystems are qualitatively distinct, so that critical processes should be differentiated from critical species (Menge and Freidenburg 2001). Here, we defined critical processes as abiotic factors that can structure communities, such as fire or frost (Menge and Freidenburg 2001). The adjective 'key' has sometimes been used to describe critical species or processes (e.g., Bond 1994, Piraino and Fanelli 1999), but we preferred to not to use it, due to the frequent confusion between 'key' and 'keystone' in the literature (e.g., Khanina 1998). Critical species may have various ecological functions in the ecosystem, and we therefore differentiated several subcategories of critical species. The first three sub-categories of critical species ('keystone', 'foundation' and 'connector' species) were defined based on their abundance and position in the food web. In contrast, the last two sub-categories ('engineer' and 'modifier' species) were defined by their relationships to the physical environment.

A species may exert a high influence on the community due to its high abundance, and may be described as a 'dominant' species (Power et al. 1996). Alternatively, a species may have strong effects on communities and ecosystems despite its low abundance, and thus be described as a 'keystone' species (Power et al. 1996, Menge and Freidenburg 2001). Keystone species are predators which strongly influence the food web structure of the community (Paine 1966, 1969a). Although keystone species may be defined by opposition to dominant species (Power et al. 1996), the disproportionate influence of a species is determined relatively, by comparison with the influence and abundance of the other species (Cottee-Jones and Whittaker 2012). Moreover, the dominance of a species is a relative notion as well, defined by comparing its biomass to the biomass of other species. Thus, the species identified as dominant may vary with the community considered within the ecosystem. For instance, Davic (2003) identified as keystone some species which were dominant within their functional group. Thus, we chose not to use the 'dominant' terminology to describe critical species, and restricted its meaning to species of high abundance in its community. Instead, we discriminated two other sub-categories of critical species, defined based on their influence on the community: 'foundation' species and 'connector' species.

Foundation species are abundant species which define the structure of the community (Dayton 1972). They also create stable conditions for other species and control ecosystem dynamics, by modulating fundamental ecosystem processes (Ellison et al. 2005, Caro 2010). Ecosystems are often named after foundation species, which are commonly low trophic level species involved in bottom-up controls, such as primary producers or habitat-forming species (e.g., redwood forests, seaweed beds or coral reefs) (Ellison et al. 2005, Sala and Knowlton 2006, Caro 2010). Note that foundation species were originally labeled as 'dominant' species (Clements 1936).

Connector species maintain the food web structure of the community, through wasp-waist controls (Cury et al. 2000). They generally correspond to abundant consumers of intermediate trophic level, such as small pelagic fish (Menge and Freidenburg 2001). They were originally described as prey supporting many predators and labeled 'key-industry' species (Elton 1927), but we called them 'connector' since they act as links between species at lower and higher trophic levels.

'Ecosystem engineers' were originally described as species that influence the availability of resources to other species by modifying living or non-living materials (Jones et al. 1994). More precisely, two types of engineer species were defined: (i) 'allogenic engineers', which modify their habitat by causing the transformation of the physical environment from one state to another, such as beavers; and (ii) 'autogenic engineers', which modify their own physical structure, such as corals (Jones et al. 1994, 1997). However, Ellison et al. (2005) established that such discrimination was unnecessary, since autogenic engineers correspond to foundation species, as defined above. Besides, some species defined as engineer species have also been described as keystone species (Barua 2011, Cottee-Jones and Whittaker 2012), notably with the introduction of the 'keystone modifier' (Mills et al. 1993) or 'earth-movers' (Bond 1994) terms. However, engineer species differ from keystone species since they modify habitat through their non-foraging activities (Jones et al. 1997, Menge and Freidenburg 2001). Thus, to avoid confusion, the alteration of living resources through herbivory should be differentiated from engineering, even when causing important modification of the habitat. Herbivore species have also been associated to keystone species in the literature (Mills et al. 1993, Bond 1994, Menge and Freidenburg 2001). Yet, grazing animals influence the community structure and ecosystem dynamics by both their feeding strategies and their physical alterations of the habitat (e.g., moose or elephant) (Naiman 1988). So, we suggested to differentiate them from both engineer and keystone species and to label them as 'modifier species'.

A supplementary sub-category of critical species could be considered: 'mutualist' species, such as seed-dispersers or pollinators. They have been described as keystone species (Mills et al. 1993), although evidence of their potential influence on the whole community was limited (Bond 1994). Indeed, mutualism consists in a reciprocally beneficial interaction between two species (Stachowicz 2001). However, in aquatic ecosystems, mutualism commonly support foundation species forming habitat (e.g., corals and zooxanthellae), so that the removal of some mutualist species could actually have community-wide consequences (Stachowicz 2001, Hay et al. 2004).

3.3.2.3 Sub-categories of surrogate species

Surrogate species are commonly described using metaphorical terms, such as 'flagship' or 'umbrella' species, which are appealing to the general public (Barua 2011). Due to the symbolic nature of the keystone term, keystone species have sometimes been associated to the metaphorical concepts used to designate surrogate species, all defined either as focal (e.g., Zacharias and Roff 2001), or as surrogate species (e.g., Favreau et al. 2006, Sergio et al. 2008). However, keystone species play a critical role in the food web, and thus correspond to a subcategory of focal species. In contrast, surrogate species may not ensure any important ecological function in their ecosystem (Armstrong and Caro 2002). Although some keystone species may be suitable tools for management (Simberloff 1998), effective surrogate species may not be keystone species (Caro and O'Doherty 1999). Moreover, there has been some semantic confusion between the different sub-categories of surrogate species: 'indicator', 'umbrella' and 'flagship' species (Caro and O'Doherty 1999, Caro 2010). However, a species useful as one type of surrogate, to achieve one particular conservation objective, will generally be unusable as another type, since species traits differ from one surrogate species to another (Caro and O'Doherty 1999).

The concept of indicator species was introduced in the literature as an index of other species attributes or environmental conditions, otherwise challenging to estimate (Landres et al. 1988). A dichotomy was later established between 'composition' indicator species (also called 'ecological' or 'environmental' indicator species) used to select areas of high biodiversity to be protected, and 'condition' indicator species (also called 'bio-indicator' or 'sentinel species') used for monitoring changes due to anthropogenic or natural disturbances (Caro and O'Doherty 1999, Zacharias and Roff 2001). For instance, species at the upper end of the food chain, such as marine mammals, are often good indicators of the health of the ecosystem (Bossart 2006).

The umbrella species concept was first coined in the 1980s, then more precisely defined in the 1990s (e.g., Noss 1990) as species with a large distribution area, so that protecting their habitat area would also protect many other naturally co-occurring species (Caro 2003, Roberge and Angelstam 2004). Due to the allometric relationship between body size and home range size, effective umbrella species are large species (Caro and O'Doherty 1999). Umbrella species are used to determine the size of areas to be protected (Caro and O'Doherty 1999, Roberge and Angelstam 2004). In practice, the concept of umbrella species appears to be more suitable for large terrestrial species (such as tiger, jaguar, or bears) (Barua 2011). Large marine species, which often are migratory species, may be more suitable as flagship species (Zacharias and Roff 2001).

Flagship species are charismatic and popular species that serve as ambassadors of broader conservations goals, often the preservation of a particular habitat or ecosystem (Heywood 1995, Caro and O'Doherty 1999, Zacharias and Roff 2001, Caro et al. 2004). The most charismatic species in ecosystems are not always the most critical to the structure and function of communities (Vanclay 1999). Thus, flagship species may be defined as mere strategic tools selected based on their symbolic or marketing value to raise public concern and encourage action and funding (Verissimo et al. 2011). So, the concept of flagship species differ from the other concepts since it is not based on any ecological foundation (i.e. flagship species do not need to meet any ecological criteria) (Caro and O'Doherty 1999, Zacharias and Roff 2001). Flagship species may encompass a wide range of examples, from the giant panda, symbol of species conservation, to the polar bear, emblem of climate change mitigation (Barua 2011).

3.3.3. Examples of sensu stricto keystone versus pseudo-keystone species

We listed examples of species commonly cited in the literature, and discriminated the ones corresponding to *sensu stricto* keystone species (Table 3.2) from pseudo-keystone species (Table 3.3).

The first classical and historical example of *sensu stricto* keystone species is the carnivorous sea star *Pisaster ochraceus* (Brandt, 1835). By feeding on the most competitive herbivorous prey in the rocky intertidal community, the mussel *Mytilus californianus* (Conrad, 1837), the sea star prevents this prey from dominating the available substrate, thereby opening it up to other less competitive prey species (Paine 1966, 1969a, 1980). The second most popular and historical example of keystone species is the sea otter *Enhydra lutris* (Linnaeus, 1758). Sea otters, by feeding on the sea urchin *Strongylocentrotus purpuratus* (Stimpson, 1857), prevent the kelp forest community from shifting (through trophic cascades) to an urchin barren dominated state (Estes and Palmisano 1974, Estes et al. 1978). Sea snails, respectively lobsters, were also shown to play the same role of keystone species as sea stars in rocky intertidal ecosystems (Duran and Castilla 1989), respectively sea otters in kelp forests (Mann and Breen 1972,

Babcock et al. 1999, Shears and Babcock 2002). Other aquatic examples of keystone species correspond to predatory fish species feeding on herbivore prey, such as basses in freshwater systems (Power et al. 1985) or sea urchin-eater fishes in coral reefs (McClanahan 1995, McClanahan 2000) and rocky reefs (Sala and Zabala 1996, Sala 1997, Clemente et al. 2010). There have been fewer terrestrial examples of *sensu stricto* keystone species proposed in the literature, with the most common one being the wolf feeding on large herbivores in temperate and boreal forests (Messier and Crête 1985, McLaren and Peterson 1994, Ripple and Larsen 2000, Beschta 2003).

The most cited example of pseudo-keystone species is the North American beaver (Barua 2011). Beavers were often labeled as keystone (habitat) modifier, although they correspond to engineer species (Jones et al. 1994). In contrast with *sensu stricto* keystone species, there have been many terrestrial examples of pseudo-keystone species. Prairie dogs are the second most cited example of pseudo-keystone species (Barua 2011). The keystoneness of several species of small rodents, such as prairie dogs, has been much debated in the literature. Small rodents, such as prairie dogs, seem to play multiple ecological roles, while mainly impacting the ecosystem as both engineer species and modifier species (Naiman 1988, Davidson et al. 2012, Cosentino et al. 2014). Elephants in African grasslands are a typical example of species cited as keystone herbivores, which would be better described as modifier species (Naiman 1988). Finally, trees in American forests have sometimes been labeled keystone plants, but would rather correspond to foundation species (Ellison et al. 2005).

3.3.4. A restrictive definition for the keystone species concept

Based on our comparative framework, we concluded that a keystone species is a high trophic level species, which has a disproportionate impact on the food web structure of its community. However, the confusion between the different concepts used in the literature to describe species of potential interest highlights the necessity of defining more precise criteria for keystone species. The three exclusive attributes of keystone species are: (1) a low abundance, so that it is likely to be a predator located at a high position in the food web; (2) a high trophic impact on its community, due to one (or few) strong and direct trophic interaction(s) established with one (or few) prey species (predation); and (3) a wide trophic impact, due to many other

indirect interactions established with many other species (predation release). The other species are themselves (directly or indirectly) interacting with the keystone species' prey and are located lower in the food web.

The restrictive definition of keystone species may encompass two different types (Figure 3.4). The first type of keystone species (KS type 1) corresponds to a situation where the keystone predator feeds on a highly competitive prey, which is competing for food or space with many other species. After removal of the keystone predator, the highly competitive prey may become a dominant species in its community. The second type (KS type 2) describes a situation where the keystone predator feeds on a prey that feeds on another prey, which provides shelter or resources to many other species. Thus, if the predator is removed, the first prey will increase in abundance (due to predation release) and the second prey and associated species will consequently decline. KS type 1 may be categorized as 'level 1', since only one intermediate prey species is involved, and describes the ecological role of sea stars or sea snails in the rocky intertidal zone. In contrast, KS type 2, involving two intermediate prey species, may be categorized as 'level 2', and depicts the role of sea-urchin feeders in kelp forests (e.g., sea otters) or coral reefs (e.g., triggerfishes).

3.4. Discussion

3.4.1. A restored concept of keystone species

In this study, we demonstrated that the concept of keystone species was ecologically relevant but commonly misused, so that the technical terminology needed to be refined. We proposed a restored definition of the keystone species concept, based on an in-depth review of the scientific literature and developed in four steps. First, we summarized the usages of the keystone species terminology in the scientific literature. We showed the expansion of its meaning over time with an evolutionary tree. Second, we extricated the keystone species concept of all overlapping concepts designating other categories of species. We proposed a comparative and descriptive framework for a clear discrimination between different species of potential interest, including keystone species. Third, we refined the widely-used concept by differentiating appropriate applications from misusages of the term in the literature. A list of the most
commonly cited pseudo-keystone species was established. Lastly, we formulated a clear and exclusive definition for keystone species, represented with a conceptual diagram.

We first described keystone species as a sub-category of ecologically important species, or critical species, defined as species with important ecological functions performed by few other species (Perry 2010). A keystone species is a unique species in terms of functional diversity, and "no other species can take over its role" (Perry 2010). Thus, the uniqueness of the keystone species appears to be one of the major factors of its importance. Yet, importance is a relative concept since species uniqueness depends on the characteristics of the other species in the ecosystem (Hurlbert 1997, Perry 2010). Prey species traits, such as competitiveness or vulnerability to predation, may be critical to the keystoneness potential of their predator (Power and Mills 1995). For instance, we identified sea urchins as dominant prey in six of the eight marine examples of keystone species. Thus, sea urchins might determine the keystone role of the few specialist predators which are able to overcome their spines (Pinnegar et al. 2000). Then, we narrowed down the concept of keystone species by defining its critical role in the food web. We defined a keystone species as a species of low abundance and high trophic level, which exerts a high and wide impact on the food web structure of its community. The restored definition of keystone species we proposed in this study is based on restrictive and specific ecological criteria, and corresponds to the original notion of 'keystone predator' (Paine 1966, 1969a, Paine 1969b).

Keystone species have been described as strong interactors in the literature (Paine 1980, Menge et al. 1994, Menge and Freidenburg 2001, Sala and Knowlton 2006). A strong interactor species has a large effect on the species with which it interacts, while a weak interactor species has a small effect on the other species (Menge and Freidenburg 2001). Other species categories were also defined as strong interactors, such as foundation species or mutualist species (Menge and Freidenburg 2001, Soulé et al. 2003). However, being a strong interactor is not a characteristic of species but depends on local conditions in the community (Caro 2010), so that weak interactors may play important ecological roles due to changing conditions (Berlow 1999). Moreover, keystone species are not characterized only by one single strong predator-prey interaction, but rather by a particular configuration of strong and weak interactions in the food web (Berlow et al. 2004).

Direct effects are defined as the influence of a species on another species resulting from their direct interaction, while indirect effects correspond to the influence of a species on another species with which it does not interact directly (Menge 1995). Direct effects may be caused by trophic (e.g., predation) or non-trophic (e.g., interference competition) interactions (or 'linkages') (Paine 1980, Menge 1995). Menge (1995) described several types of indirect effects corresponding to trophic interactions, including (among others): (i) 'keystone predation', when a predator indirectly increases the abundance of competitors of its prey via consumption of the highly competitive prey; and (ii) 'trophic cascade' (or 'tri-trophic interaction'), when an increase in plant abundance is caused by the control of herbivores by a predator. Based on the latter definitions, the KS type 1 proposed in this study would correspond to keystone predation, while the KS type 2 would be better described as a trophic cascade. However, Menge (1995) recognized that trophic cascades and keystone predation could also be seen as "different versions of the same type of indirect interactions", which may actually be comparable. Also, Pinnegar et al. (2000) defined trophic cascades as "predatory interactions involving three trophic levels", and keystone predation as a "three-species interaction involving competition". Thus, depending on whether we define trophic cascades based on the number of species interactions involved (including trophic and non-trophic interactions) or the number of trophic interactions only, keystone species may be, either assimilated to, or differentiated from, trophic cascades.

In our approach, we chose to assimilate the KS type 2 to a keystone species, rather than a trophic cascade. Indeed, the keystoneness of the KS type 2 predator species is not only due to predatory interactions cascading through the food web, but may also be due to the indirect effect of habitat facilitation. Habitat facilitation was defined as the situation where a species indirectly improves the habitat of another species by altering the abundance of a third species that has a negative effect on the habitat (Menge 1995). Thus, here, the KS type 2 predator feeds on the prey that feeds on the host species on which many other species depend, and thus provides habitat facilitation to these species. Alternatively, the KS type 2 situation could be seen as a trophic cascade that involves the removal of a foundation species.

3.4.2. Context-dependency issues with the keystone species concept

When dealing with keystone species (or species functional roles in general), ecologists face the issue of context-dependency: a species may or may not be keystone depending on the ecosystem where it is encountered (Power et al. 1996, Arponen 2012). Several authors acknowledged that *a-priori* identifying keystone species with confidence was a difficult task (Paine 1995, Power and Mills 1995, Power et al. 1996). Some authors demonstrated that species taxonomy could determine keystoneness, due to inherent and intrinsic evolutionary attributes (Stouffer et al. 2012). In contrast, other authors argued that species are keystone under certain conditions only, so that there would be no absolute species-specific property to be keystone (Mills et al. 1993, Paine 1995, Power and Mills 1995). Thus, identifying keystone species would require documenting species abundances, diets and interactions over various environmental conditions (Power et al. 1996). For instance, a comparative analysis of two Eastern Pacific rocky intertidal food webs demonstrated regional changes in the pattern of trophic interactions between the same species (Paine 1980). Menge et al. (1994) concluded that there are no systematic keystone species and that the keystoneness status varies across space. However, the variability in space and time of the species ecological roles is not easy to capture, as illustrated by the two following quotes by R.T. Paine: "All species play some role, albeit generally unknown, at some place or time" (Paine 1995); and "Food webs are idealized pictures of complex trophic patterns that change seasonally and geographically" (Paine 1980).

The keystone status of a species depends on a suite of biotic and abiotic factors determining the distribution and abundance of species in space and time (Harley 2011). Species may or may not be keystone, depending on changes in their own population over time (Piraino et al. 2002). Thus, attempts to discriminate between 'keystone' species and 'dominant' or 'rare' species were claimed to be irrelevant, seeing that keystone species could be more or less abundant over time (Christianou and Ebenman 2005). Environmental variability may also influence the ecological role of a particular species in its ecosystem by modifying species interactions strength (Paine 1966, 1980, Power et al. 1996). Abiotic variables may include physical factors, such as temperature or topology (Paine 1966), but also productivity or disturbance (Power et al. 1996). Changes in temperature may induce direct effects on species distribution and abundance, as well as indirect effects on species interactions (Poloczanska et al.

2008). As a result, small changes in climate could generate large modifications in community composition and structure (Harley 2011) and influence species keystoneness (Sanford 1999, Christianou and Ebenman 2005). This is particularly the case in rocky intertidal communities where organisms already live close to their thermal tolerance limits (Harley 2011), and where experiments showed that slight fluctuations in water temperature regulate the impact of a keystone predator on its principal prey (Sanford 1999).

3.4.3. 'Keystone species': more than an ecological concept?

In our approach, we defined keystone species exclusively based on ecological criteria, but other types of criteria could potentially be considered. Anthropologists suggested including the cultural value of species as a criterion to select keystone species. They introduced the extended concept of 'cultural keystone species', defined as a species essential to the sustainability of socio-ecological systems (Cristancho and Vining 2004, Garibaldi and Turner 2004, Platten and Henfrey 2009). Cultural keystone were defined as species whose removal could dramatically change human (and especially indigenous) communities, which depend on them to maintain their cultures, and for which they may have nutritional, medicinal or spiritual values (Cristancho and Vining 2004, Garibaldi and Turner 2004).

However, the cultural keystone species concept has also been criticized in the literature. Davic (2004) argued that the definition of cultural keystone species was in contradiction with the original meaning of the ecological concept, and that culturally important species should not be associated to keystone species, but rather to flagship species. Nunez and Simberloff (2005) discussed the potential risks and benefits of applying the cultural keystone species concept. On one hand, conservation approaches based on cultural keystone species may be more successful due to the increased participation of local human communities (Nuñez and Simberloff 2005). For instance, cultural keystone species may stimulate co-management between indigenous and government stakeholders for a better integration of traditional knowledge (Butler et al. 2012). On the other hand, culturally important species may correspond to invasive species, so that the application of the cultural keystone species concept could turn out to be counter-productive for biological conservation (Nuñez and Simberloff 2005).

Biodiversity conservation is facing the Noah's Ark problem of "efficiently allocating limited funds to conserve biodiversity" (Perry 2010). As a consequence, trade-offs between benefits and costs should be considered before the implementation of a particular approach to conservation (Wiens et al. 2008). Due to their critical role in the ecosystem, keystone species (and other species of potential interest) could be used to prioritize conservation actions (Arponen 2012). Approaches based on focal or surrogate species may reduce costs by reducing the number of species to monitor and simplifying communication (Wiens et al. 2008). However, these approaches may take years to be beneficial (Caro 2010).Thus, conservation policies based on the concept of keystone species (and other species of potential interest) should be prioritized based on relevant economic criteria, such as cost-effectiveness (Arponen 2012).

Despite the complexity and subjectivity of assigning economic values to species, four classic criteria may be used: intrinsic value, aesthetic value, direct value as resources on the marketplace, and indirect value through maintenance of ecosystem services (De Leo and Levin 1997). The latter four criteria were merged into the notion of total economic value of species, and used for identifying ecologically important species, while ensuring the cost-effectiveness of the resultant species protection measures (Perry 2010).

In theory, species prioritization is science-based and objective, but, in practice, the choice of species to be prioritized for conservation is often subjective and based on real-world constraints (Arponen 2012). Indeed, managers need to include practical criteria when using focal or surrogate species for conservation planning and management (Sergio et al. 2008). For instance, avoiding species generating local conflict, focusing on well-known species, and preferentially selecting species with intrinsic value and easy to monitor, may help for a better efficacy of focal and surrogate species as conservation tools (Sergio et al. 2008). Besides, the main issue with management approaches based on species of potential ecological or managerial interest relates to context-dependency (e.g., Zacharias and Roff 2001, Sergio et al. 2008, Caro 2010). Thus, the temporal and spatial scales on which such approaches could be efficiently applied should be investigated and determined (Favreau et al. 2006). Finally, in response to the arguments against the use of the keystone species concept for management (Zacharias and Roff 2001), we would recommend that the concept should be applied on local scale, based on ecosystem-specific thresholds, and only when appropriate and useful regarding the conservation objectives.

Concept	Original term	Reference(s)	Definition	Interest	Reference(s)	Example(s)	Reference(s)
Focal	Focal species	(Lambeck	Species which are selected	Species of importance to	(Armstrong	See sub-categor	ies below
species		1997)	to preferentially focus on,	its ecosystem	and Caro		
			among all species in the		2002)		
			community				
Critical	Ecologically	(Perry 2010)	Focal species of ecological	Species that play an	(Perry 2010)	See sub-categor	ies below
species	important		importance, so that the	important role for the			
	species		absence of these species	structure, composition or			
			would lead the loss of many	functioning of its			
			others	ecosystem			
Keystone	Keystone	(Paine 1966,	Consumers of high trophic	Species that maintain the	(Paine 1966,	See Table 3.2	
species	predator	1969a)	level whose effects are	food web structure of the	1969a)		
			disproportionately large	community			
			relative to their abundance				
Connector	Key-industry	(Elton 1927)	Abundant consumers of	Species that maintain the	(Cury et al.	Small pelagic	(Menge and
species	species		intermediate trophic level,	food web structure of the	2000, Menge	fish	Freidenburg
			that act as links between	community	and		2001)
			species at lower and higher		Freidenburg		
			trophic levels		2001)		
Foundation	Dominant	(Clements	Abundant, low trophic	Species that define	(Ellison et al.	Redwood	(Ellison et
species	species;	1936);	level, primary producers or	community structure,	2005, Caro	forests;	al. 2005,
	Foundation	(Dayton	habitat-forming species	create stable	2010)	seaweed beds;	Caro 2010)
	species;	1972); (Jones		environmental conditions,		coral reefs	
	Autogenic	et al. 1994)		and control ecosystem			
	engineers			dynamics			

Table 3.1. Comparative framework describing 12 categories of species of potential interest, based on a literature review.

Concept	Original term	Reference(s)	Definition	Interest	Reference(s)	Example(s)	Reference(s)
Engineer	Keystone	(Mills et al.	Species causing the	Species that cause (Jones et al.		Beavers;	(Jones et al.
species	modifiers; Earth-	1993); (Bond	transformation of the	important modification to 1994, 1997)		woodpeckers	1994)
	movers;	1994); (Jones	physical environment from	the habitat and thus			
	Allogenic	et al. 1994)	one state to another,	influence the availability			
	engineers		through their non-foraging	of resources to other	of resources to other		
			activities	species			
Modifier	Keystone	(Mills et al.	Herbivore species that	Species that cause	(Naiman 1988)	Moose;	(Naiman
species	herbivores;	1993); (Jones	modify the physical	important modification to		elephant	1988)
	Allogenic	et al. 1994)	environment by both their	the habitat and thus			
	engineers		feeding strategies and their	influence the availability			
			physical alterations of the	of resources to other			
			habitat	species			
Mutualist	Mobile links;	(Gilbert 1980);	Species that establish a	Species that may support	(Stachowicz	Corals and	(Stachowicz
species	Mutualists	(Boucher et al.	reciprocally beneficial	habitat-forming species	2001, Hay et	zooxanthellae;	2001, Hay et
		1982)	interaction with another		al. 2004)	mangroves	al. 2004)
			species			and sponges	
Surrogate	Surrogate	(Caro and	Species that are substitute	Species which may not	(Caro and	See sub-categor	ies below
species	species	O'Doherty	for something else	ensure any important	O'Doherty		
		1999)		ecological function, but	1999,		
				are used as tools to	Armstrong and		
				achieve another purpose	Caro 2002)		
	1		1			1	

Concept	Original term	Reference(s)	Definition	Interest	Reference(s)	Example(s)	Reference(s)
Indicator	Indicator species	(Landres et al.	Species that are used as an	Species that may be used (Caro and		Marine	(Bossart
species		1988)	index of other species	for selecting areas to be	O'Doherty	mammals	2006)
			attributes or environmental	protected or monitoring	1999,		
			conditions, otherwise	effects of anthropogenic	Zacharias and		
			challenging to estimate	or natural disturbances	Roff 2001)		
Umbrella	Umbrella species	(Noss 1990)	Species with a large	Species that may be used	(Caro and	Tiger; jaguar;	(Barua
species			distribution area, so that	to determine the size of	O'Doherty	bears	2011)
			protecting their habitat area	areas to be protected	1999, Caro		
			would also protect many		2003, Roberge		
			other naturally co-occurring		and Angelstam		
			species		2004)		
Flagship	Flagship species	(Heywood	Charismatic and popular	Species with a symbolic or	(Caro and	Giant panda;	(Barua
species		1995)	species	marketing value, that may	O'Doherty	polar bear	2011)
				serve as ambassadors of	1999, Caro et		
				broader conservation goals	al. 2004,		
					Verissimo et		
					al. 2011)		

Table 3.2. List of examples of species labeled as 'keystone predator' or 'keystone species' (*Sensu* Paine 1966, 1969). * indicates that the term 'keystone' was not explicitly mentioned by the authors in the references, although the described predator species corresponded to a 'keystone species' (*Sensu* Paine 1966, 1969).

Keystone species	Dominant prey	Ecosystem type	Study area	References
Bass (Micropterus spp.)	Minnow (Campostoma anomalum)	Freshwater (stream)	North America	(Power et al. 1985) *
Lobster (Homarus americanus)	Sea urchin (Strongylocentrotus spp.)	Marine (kelp forest)	Eastern Canada	(Mann and Breen 1972)
Lobster (Jasus edwarsii)	Sea urchin (Evechinus chloroticus)	Marine (kelp forest)	New Zealand	(Babcock et al. 1999, Shears and
				Babcock 2002)
Sea otter (Enhydra lutris)	Sea urchin (Strongylocentrotus spp.)	Marine (kelp forest)	California;	(Estes and Palmisano 1974, Estes et al.
			Alaska	1978)
Sea snail (Concholepas	Mussel (Perumytilus purpuratus)	Marine (rocky	Chile	(Duran and Castilla 1989)
concholepas)		intertidal)		
Sea star (Pisaster ochraceus)	Mussel (Mytilus californianus)	Marine (rocky	Washington;	(Navarrete and Menge 1996)
		intertidal)	Oregon	
Triggerfish (Balistapus	Sea urchin (Echinometra mathaei)	Marine (coral reef)	Kenya	(McClanahan 1995, McClanahan 2000)
undulatus)				
Triggerfish (Balistes capriscus)	Sea urchin (Diadema antillarum)	Marine (rocky reef)	Canary Islands	(Clemente et al. 2010)
Seabream (Diplodus spp.)	Sea urchin (Paracentrotus lividus)	Marine (rocky reef)	Mediterranean	(Sala and Zabala 1996, Sala 1997) *
Wolf (Canis lupus)	Elk (Cervus elaphus)	Terrestrial (forest)	North America	(Ripple and Larsen 2000, Beschta 2003)
Wolf (Canis lupus)	Moose (Alces alces)	Terrestrial (forest)	North America	(Messier and Crête 1985, McLaren and
				Peterson 1994) *

Table 3.3. List of examples of 'pseudo-keystone' species, i.e. species labeled as 'keystone' in the literature but whose description would rather correspond to other categories of species of potential interest. * indicates that the term 'keystone' was used in the references, but the other species categories to which they are associated in this table was also used or described.

Pseudo-	Labels in the literature	Ecosystem type	Study area	Species category	References
keystone					
species					
Beavers	Keystone modifier (Mills et al. 1993, Cottee-Jones and	Freshwater	North	Engineer species	(Jones et al. 1994)
	Whittaker 2012); Earth-mover (Bond 1994); Habitat	(wetland)	America		
	modifier (Menge and Freidenburg 2001)				
Elephants	Keystone herbivore (Mills et al. 1993, Bond 1994);	Terrestrial	Africa	Modifier species	(Naiman 1988)
	Ecosystem engineers (Soulé et al. 2003, Cottee-Jones	(grassland)			
	and Whittaker 2012)				
Kangaroo rats	Keystone herbivore (Mills et al. 1993); Keystone	Terrestrial	North	Engineer species;	(Cosentino et al. 2014)*
	predator (Bond 1994); Habitat modifier (Menge and	(desert)	America	Modifier species	
	Freidenburg 2001)				
Prairie dogs	Habitat modifier (Menge and Freidenburg 2001)	Terrestrial	North	Engineer species;	(Naiman 1988);
		(grassland)	America	Modifier species	(Davidson et al. 2012) *
Trees	Keystone plant/host (Mills et al. 1993); Keystone plant	Terrestrial	America	Foundation species	(Ellison et al. 2005)
	resource (Bond 1994, Cottee-Jones and Whittaker	(forest)			
	2012); Keystone plant (Menge and Freidenburg 2001);				
	Keystone mutualist (Cottee-Jones and Whittaker 2012)				
	1			1	



Figure 3.1. Evolutionary tree representing the evolution of the keystone species concept over time, based on a literature review. Since the introduction of the original definition (1), the concept has evolved toward an inclusive (2) and then extended (3) definition, and has been applied for non-ecological considerations (4). All terms are organized on the tree based on the year of publication of their corresponding references.

RELATIONSHIPS



Figure 3.2. Comparative framework of the 12 categories of species of potential interest, classified by category and represented based on their potential interests (i.e. relevance as a management tool or importance due to ecological role, at the species, community, or habitat scales).



Figure 3.3. Comparative framework of the 12 categories of species of potential interest, distributed on trophic level *versus* biomass scales. The keystone species category is highlighted in bold.

BEFORE REMOVAL

AFTER REMOVAL



Figure 3.4. Conceptual diagram representing the restored definition of the keystone species concept. Both types of keystone species (KS type 1 and KS type 2) are represented before and after the removal of the keystone species. The different types of arrow represent different types of species interactions and the size of the boxes represents species abundance.

4. Keystone species: toward an operational concept for marine biodiversity conservation

4.1. Introduction

The metaphorical terminology of 'keystone species' was introduced in aquatic food web ecology by R.T. Paine (1969a, 1969b). A keystone species was first described as a predator maintaining high species diversity and complex interspecific feeding relationships in the community (Paine 1966). Variations in the keystone species abundance or activity would have greater impacts on biodiversity and trophic structure, compared to other coexisting species with similar or higher abundance in the ecosystem (Paine 1969a, Paine 1969b). Since Paine's analogy, the concept of keystone species rapidly expanded, as it was applied to an ever-growing number of aquatic and terrestrial species, playing a wide variety of critical roles in the ecosystem (Paine 1995, Power and Mills 1995, Power et al. 1996). Many authors discussed the relevance of the keystone species term turned into an inclusive concept (Hurlbert 1997), which has been either described as a powerful buzzword in conservation (Barua 2011), or criticized as an ambiguous and overused concept (Cottee-Jones and Whittaker 2012). As pointed out by Paine (1995): "an answer serving all masters probably provides few useful solutions". Thus, in this study, a clear, exclusive, and thus operational, definition of the keystone species was applied, based on the original concept of 'keystone predator' (Paine 1966, 1969a). More precisely, we defined a keystone species as a predator species which disproportionately influence the food web structure of its community. In other words, we considered that a keystone species correspond to a predator species with a high and wide impact on its food web, despite a low biomass.

Experts reviewed the methods used to identify keystone species and concluded that the most powerful approach was the combination of comparative studies with experimental methods (Power et al. 1996), as conducted by several authors (e.g., Paine 1966, Menge et al. 1994). However, field experiments have practical limitations. Field-based experimental removals of single species are expensive and time-consuming, restricted in scope (both spatially and temporally), and may be challenging with some types of species (either not easily accessible, or under some restrictive protection statuses) (Power et al. 1996, Bond 2001, Libralato et al. 2006).

Thus, experimental approaches often require focusing on a few species only, a-priori assumed to be the potential keystone ones, which may introduces bias in the analysis of keystoneness (Libralato et al. 2006). To overcome these difficulties, recent approaches to identify potential keystone species were based on a variety of ecological modeling methods: ecological network analysis (ENA) (Jordán et al. 1999, Estrada 2007, Jordán et al. 2007, 2009, Torres-Alruiz and Rodríguez 2013); loop analysis (e.g., Ortiz et al. 2013a, Ortiz et al. 2013b); community viability analysis (e.g., Christianou and Ebenman 2005, Ebenman and Jonsson 2005, Berg et al. 2011, Stouffer et al. 2012); or food web models (e.g., Okey et al. 2004, Libralato et al. 2006, Eddy et al. 2014).

Different indices measuring the potential of species to be critical to the community were proposed and reviewed in the literature (Jordán et al. 2008, Jordán 2009, Perry 2010, Cottee-Jones and Whittaker 2012). Initially, the proposed indices were based, either on observations from the field (e.g., interaction strength (Paine 1992) or community importance (Mills et al. 1993, Power et al. 1996)), or on theoretical concepts (e.g., general functional importance (Hurlbert 1997) or functional group dominance (Davic 2003)). A suite of structural indices, derived from binary or weighted networks, was then developed: degree (Jordán et al. 2003, Scotti et al. 2007), centrality indices (Estrada 2007), overlap indices (Jordán 2009), topological importance of species (Jordán et al. 2008), trophic function and trophic field overlap (Jordán et al. 2009). Recently, a topo-dynamical criterion, which estimates the consequences of species removal on community dynamics, was proposed in the ENA literature (Torres-Alruiz and Rodríguez 2013). Besides, qualitative indices, based on loop analysis models, were introduced and compared to existing structural and functional indices (Ortiz et al. 2013a, Ortiz et al. 2013b). Three indices explicitly quantifying species keystoneness were proposed: a structural index (K), based on network analysis (Jordan et al. 1999); a dynamic index (KI), based on time-dynamic simulations (Okey et al. 2004); and a functional index (KS), based on mass-balanced modeling (Libralato et al. 2006).

In this study, we used the Ecopath with Ecosim (EwE) modeling approach to estimate species keystoneness and identify potential keystone species in marine communities. EwE is a well-known and widely-applied modeling approach in aquatic ecology (Coll et al. 2008, Christensen et al. 2011). The EwE software is freely accessible (www.ecopath.org) and

published EwE models become more and more accessible, so that the approach has been applied to hundreds of aquatic ecosystems worldwide and several meta-analysis, based on EwE models, have already been published (Colléter et al. 2013b). EwE-based studies help understanding the general structure and functioning of aquatic ecosystems, by summarizing the available knowledge on a given ecosystem, deriving its various system properties, and comparing them to other ecosystems (Walters et al. 1997). The EwE modeling approach was primarily developed to answer 'what if' questions about policy that could not be addressed with single-species assessment models (Christensen and Walters 2004). Thus, EwE is more suitable to study aquatic food webs than terrestrial ones and has been primarily applied to marine ecosystems. In this study, we only considered EwE models representing marine ecosystems.

EwE may be described as an ecosystem model since it represents feeding relationships between all species occurring in the ecosystem, although it only captures trophic interactions, not nutrient cycling. EwE is based on ECOPATH, a food web model first proposed and applied to estimate the main predator-prey pathways in the marine ecosystem of Northwestern Hawaiian Islands (Polovina 1984). The original ECOPATH model was then developed further (Christensen and Pauly 1992), and turned into the EwE modeling complex, which can be seen as a tool-box offering a large collection of methods to analyze various ecological phenomena. The EwE modeling complex consists of a suite of three main sub-models: (i) Ecopath, static and descriptive; (ii) Ecosim, dynamic and predictive; (iii) Ecospace, spatially explicit, dynamic and predictive (Christensen and Walters 2004). Ecopath is a descriptive model, representing a static snapshot of the ecosystem trophic structure, and used as a parameter estimation methodology in the EwE modeling complex (Walters et al. 1997). Ecosim uses the outputs of Ecopath to produce time-dynamic simulations of changing trophic interactions with changes in the ecosystem due to anthropogenic or environmental disturbances (Walters et al. 1997). Ecosim may be used to fit model predictions to time-series data, and to explore different fisheries management or climate change scenarios (Christensen and Walters 2004). Ecospace replicates outputs of Ecosim over a spatial grid to explicitly account for the spatial aspects of trophic structure, and was primarily designed for exploring the possible consequences of alternative marine protected areas policies (Walters et al. 1999).

In this study, we focused on three main questions related to the identification of keystone species in marine ecosystems: (1) What are the limitations of the existing functional indices measuring species keystoneness? (2) Could these limitations explain the inconsistencies and discrepancies observed when applying these indices to modeled food webs? (3) How could we formulate a new functional index overcoming these limitations? We intended to answer these questions based on a meta-analysis of published Ecopath models representing marine food webs. First, models were selected with a scoring method. Second, several indices of keystoneness were formulated, comprising new and existing ones. Third, the indices were applied to the models, and the obtained keystone species were recorded. A preliminary comparison of the results was made to identify potential biases in the indices. Then, two statistical methods were used to select the most suitable index: Spearman rank correlation tests and a classification tree. The new functional index of keystoneness was selected according to the indicated definition of keystone species and applied to a well-known case study.

4.2. Methods

4.2.1. Derivation of indices of keystoneness from Ecopath food web models

4.2.1.1 Selection of the Ecopath models with a scoring method

The data used in this study was extracted from 101 Ecopath models. First, the EcoBase database was used to establish the list of models to select. EcoBase is an online repository, referencing and integrating information from more than 400 published EwE models (Colléter et al. 2013b). We extracted critical metadata on the models stored in EcoBase, and reused some of the metadata as selection criteria in our analysis. Then, the data extracted from the selected models were accessed through another collection of EwE models (Christensen et al. 2011).

We collected from EcoBase a suite of metadata including the ecosystem type, the climatic zone, the first and last year, the spatial extent and the reference of the models. We excluded from our analysis all referenced models representing non-marine ecosystem types. Among the marine types, models were selected by applying a scoring method, based on six

criteria: (1) an analysis of keystone species (*KS*) was previously performed with this model; (2) the model represented an established Marine Protected Area (MPA); (3) another (or more) historical version(s) (called 'sibling') of the same modeled ecosystem was available; (4) the model was focusing on a species (or group of species) of particular interest; (5) detailed information on species aggregation into functional groups was available for this model; (6) another (or more) geographical version(s) (called 'Overlapping') of the same modeled ecosystem was available. We note that criteria 1, 2 and 3 were particularly relevant to our study, whereas criteria 4, 5 and 6 were less significant. Indeed Outcomes from past analyses of keystone species on the same ecosystems could be confronted to our results. Models representing MPAs, or successive historical versions of the same area, could be used to understand fishing impact on marine food webs and keystone species. In contrast, species of particular interest might or might not help identifying keystone species. Overlapping models were actually very few in the EcoBase database.

All criteria correspond to metadata directly extracted from EcoBase, apart from criteria 3 and 6, which were refined for the purpose of this study. Sibling models (criteria 3) were more precisely defined here as models with the same geographic location and surface area, but representing different years or time periods. Overlapping models (criteria 6) were defined as models with the same geographic location and time period, but not necessarily the same surface area (i.e. representing the ecosystem at smaller or larger spatial scales). Each criterion was given a score of 1 if true, and 0 if false. For each model, the final score was obtained by summing the scores of the six criteria, with a coefficient of 2 applied to the first three criteria, since they were more relevant to this study. The final scores ranged from 0 to 6. Models were selected only if their final score was equal to or higher than 3. Nonetheless, models with an overall score lower than 3, but a positive score for one of the first three criteria (of higher importance), were also considered.

4.2.1.2 Description of the Ecopath modeling approach

Ecopath describes the feeding relationships between all species occurring in the modeled food web (see Appendix B (Figure B1) for an example). Species are aggregated into functional

(or trophic) groups, corresponding to an age/size class of a single species, a single species, or a group of species sharing similar ecological traits (such as size, diet, predator and life cycle) (Christensen et al. 2008). A functional group can also be defined as a group of species with similar effects on ecosystem processes, without redundancy among the other groups (Perry 2010). Thus, a keystone species may be represented by a functional group (De Leo and Levin 1997, Perry 2010), or by the most abundant species within its functional group (Davic 2003). As a result, the terminologies 'keystone groups' and 'keystone species' are used likewise in this study.

The main assumption in Ecopath is of mass balance over a given time period (typically one year) (Christensen and Walters 2004). For each functional group, Ecopath assumes that the energy input and output are balanced in the ecosystem, and that the system has the same biomass state at the end of the period as it had at the beginning (Walters et al. 1997). The mass-balance constraint serves as a filter for mutually incompatible estimates in the model. All available information collected about the components of the ecosystem pass through the 'mass balance filter', which determines what parameters must be to support the current trophic structure and be consistent with observations (Walters et al. 1997, Christensen and Walters 2004).

For each selected Ecopath model, we gathered, from the collection of EwE models (Christensen et al. 2011), the name and biomass $(B, t \cdot km^{-2})$ of each living group (dead groups, such as detritus, were excluded), and deduced the total number of living groups in the model and their total biomass in the ecosystem $(B_{tot}, t \cdot km^{-2})$. Biomass is usually entered as input data in Ecopath, but may be estimated by the model if missing. As a first data quality check, we recorded the number of biomass estimates computed by Ecopath for each model (B_{estim}) , and deduced the proportion of estimated biomass. Although we did not use Ecosim in our analysis, we recorded for each selected model, if the Ecopath model was fitted to time series in Ecosim or not (metadata extracted from EcoBase), and used it as a second data quality check. A supplementary parameter, the trophic level (*TL*, dimensionless), was collected for each functional group in each selected model. *TL* is a fractional number giving the position of each functional group in its food web (generally ranging from 1 to 5), and estimated by Ecopath based on the diet composition of the group and the *TL* of its prey items (starting with a *TL* of 1 assigned to producers and detritus) (Christensen and Pauly 1992). Some of the selected models described ecosystems exploited by one or more fishing fleets. For these models, we collected the total

number of fishing fleets in the model and the total catch rate $(Y_{tot}, t \cdot km^{-2} \cdot year^{-1})$ of all fishing fleets in the ecosystem. The mean trophic level of the catch $(TL_Y, dimensionless)$, estimated by Ecopath based on the composition of the total catch and the *TL* of the targeted groups (Christensen et al. 2008), was collected as well.

4.2.1.3 Description of the Mixed Trophic Impact (MTI) analysis and derived indices of keystoneness (KS)

Several modules were developed and added to the EwE package, such as the 'Network Analysis' module, a tool available with the Ecopath model (Christensen et al. 2008). The Network Analysis notably comprises the 'Mixed Trophic Impact' (see Appendix B (Figure B2) for an example) and 'Keystoneness' (KS) analyses. The Mixed Trophic Impact (MTI) is an economic input-output analysis adapted to ecological networks by Ulanowicz and Puccia (1990), and implemented in Ecopath (Christensen and Walters 2004). The MTI is calculated by constructing an $n \times n$ matrix, whose elements (m_{ij}) represent, for each pair of groups (i, j) in the modeled food web, the relative impact of the impacting group i on the impacted group j, by considering direct (predation) and indirect (competition) feeding interactions (Ulanowicz and Puccia 1990, Christensen and Walters 2004).

The elements (m_{ij}) of the MTI matrix represent the relative mixed trophic impact of the impacting group *i* on the impacted group *j*, for each pair of groups (i, j) in the modeled food web. The m_{ij} are derived from the net impact (q_{ij}) of group *i* on group *j*, for all the possible pathways that link both groups in the food web (Ulanowicz and Puccia 1990, Libralato et al. 2006). The q_{ij} are calculated by the difference between positive effects, quantified by a diet composition term (DC_{ji}) , and negative effects, expressed by a host composition term (FC_{ij}) : $q_{ij} = DC_{ji} - FC_{ij}$ Equation 4.1

Where DC_{ji} is the proportion of group *i* in the diet of group *j*, and FC_{ij} is the proportion of group *j* in the consumption by group *i* (Ulanowicz and Puccia 1990, Christensen and Walters 2004). For dead groups, DC_{ji} is set to zero, while for fishing fleets, DC_{ji} represents the proportion of group *i* in the catch of fleet *j* (Christensen et al. 2008). The m_{ij} are estimated for each fishing fleet defined in the model, by considering fishing fleets as predators (Christensen and Walters 2004).

Two alternative indices measuring the potential for being a keystone species, or 'keystoneness' (KS), were implemented in the Keystoneness analysis of the Network Analysis module in EwE (Christensen et al. 2008). The first index (called KS#1 in EwE) was proposed by Libralato *et al.* (2006), and the second one (called KS#2 in EwE) was adapted from a methodology proposed by Power *et al.* (1996). Both indices are estimated based on the same parameters: a measure of trophic impact (ε_i) derived from the MTI analysis, and a measure of biomass (p_i). ε_i represents the overall effect of group *i* on all the other groups in the food web (without including the effect of the group on itself):

$$\varepsilon_i = \sqrt{\sum_{j \neq i} m_{ij}^2}$$
 Equation 4.2

Where ε_i is expressed as the sum of the squared values of m_{ij} of group *i*, paired with each of the other living group *j* in the food web. The mixed trophic impact of group *i* on itself (m_{ii}) are excluded, as well as the mixed trophic impact on dead groups such as detritus (Libralato et al. 2006).

p_i corresponds to the contribution of group *i* to the total biomass in the food web:

$$p_i = \frac{B_i}{\sum_{k=1}^n B_k}$$
Equation 4.3

Where B_i is the biomass of group *i*, and B_k the biomass of each of the *n* living groups in the food web (Power et al. 1996, Libralato et al. 2006).

The KS#1 and KS#2 indices are obtained by combining ε_i and p_i for each group *i* (Power et al. 1996, Libralato et al. 2006), such as:

$$KS#1_i = \log[\varepsilon_i \times (1 - p_i)]$$
Equation 4.4
$$KS#2_i = \log[\varepsilon_i \times (1/p_i)]$$
Equation 4.5

4.2.1.4 Formulation and application of several KS indices

In both KS#1 and KS#2 indices, the keystoneness is estimated based on two components: (i) a component estimating the trophic impact of the group (here called Impact Component (IC)); and (ii) a component estimating the biomass of the group (here called Biomass Component (BC)), so that a general equation for an index of keystoneness (KS) may be expressed:

 $KS_i = \log[IC_i \times BC_i]$

Equation 4.6

Based on the general equation of KS (Equation 4.5), we explored several formulations and combinations of IC and BC. We retained three different ICs and four different BCs, and combined the seven components in all possible ways to obtain 12 alternative KS indices (Table 4.1). ICs were calculated using a measure of trophic impact (ε_i) (Equation 4.2), and BCs using a measure of biomass (B_i) (Equation 4.3). To avoid imbalance between both components, BCs and ICs were defined so that they had value ranges of comparable order of magnitude. One of the ICs and two of the BCs were directly adapted from the literature (Power et al. 1996, Libralato et al. 2006) and called using a subscript capital letters (IC_L , BC_L , BC_P), while the other components were called using subscript numbers, with a zero for the components using ranks (IC_0 and BC_0). Note that two of the 12 KS indices (KS_1 and KS_2) were directly adapted from the literature and correspond to the KS#1 and KS#2 indices described above (Equation 4.4 and Equation 4.5).

The 12 retained KS indices were applied to the 101 selected modeled ecosystems. The names of the groups with the highest value of keystoneness were recorded for each KS index and each model. The m_{ij} values were extracted from Ecopath for each living functional group (dead groups such as detritus were not considered) of each selected model, and ε_i was calculated as described above (Equation 4.2). p_i was derived from the B_i values extracted from Ecopath, as described above (Equation 4.3). Contrary to previous approaches (e.g., Libralato et al. 2006), the m_{ij} corresponding to fishing fleets were included in our analysis. We assumed that fishing fleets could be added as a supplementary functional group, if considered as a predator feeding on targeted groups. Therefore, a supplementary group, called 'All Fleets', was added as a n + 1 functional group, in all selected models representing exploited ecosystems. All defined fishing fleets were combined together into the 'All Fleets' group, whose B_i and TL_i were approximated with the Y_{tot} and TL_Y , respectively. For models with multiple fleets, m_{ij} of All Fleets was obtained by summing up the m_{ij} values over all the defined fishing fleets.

4.2.2. Analysis of the contributions of the IC and BC components to the keystoneness estimation

4.2.2.1 Comparison of groups ordered by keystoneness, trophic impact and biomass

To test the 12 KS indices defined above (Table 4.1), we analyzed the balance between IC and BC components for each index. First, we compared, for each KS index and each selected model, the groups ordered by keystoneness, with the groups ordered by trophic impact and biomass, separately. Precisely, we compared the group of the highest keystoneness with: (i) the three groups with the highest values of trophic impact (ε_i); and (ii) the three groups with the lowest values of biomass (B_i) . If the group with the highest keystoneness value also had one of the three highest trophic impact values, then the model was categorized as 'Match Impact' for the particular index. In contrast, if the group with the highest keystoneness value also had one of the three lowest biomass values, then the model was categorized as 'Match Biomass' for the particular index. If the group with the highest keystoneness did not correspond to any of the three groups, neither with the highest trophic impact, nor with the lowest biomass, then the model was categorized as 'No Match' for the particular index. The methodology was applied to each of the 101 selected models, and the number of models in each matching category (Match Biomass, Match Impact or No Match) was recorded, for each KS index. The 'Overall Match', obtained for each KS index over all models, corresponded to the matching category of the majority of models (i.e. 51 models or more, for a total of 101 models).

4.2.2.2 Rank correlation tests between KS indices and trophic impact or biomass estimates

To analyze further the balance between IC and BC components for each KS index, we applied the Spearman's rank correlation test (Coleman 2010) using the R software (<u>www.r-project.org/</u>). We tested if there was a monotonic correlation between the rank (in ascending order, because keystone species should have high keystoneness) of the KS index of group *i*, called $arank(KS_i)$, and: (1) the rank (in ascending order, because keystone species should have

high trophic impact) of the trophic impact of group *i*, called $arank(\varepsilon_i^2)$; and (2) the rank (in descending order, since keystone species should have low biomass) of the biomass of group *i*, called $drank(B_i)$. The Spearman's rank correlation test was applied twice (once with the trophic impact, and once with the biomass) to each KS index. The rank correlation tests were validated for each model, if and only if, for the particular KS index: (i) the hypothesis *H*1 (i.e. there is a monotonic correlation) of the Spearman's rank correlation test was validated (i.e. *p-value < 0.05)* for both tests 1 and 2; (ii) the coefficient of correlation *r* was positive for both tests 1 and 2; and (iii) the correlation coefficients r_1 and r_2 of tests 1 and 2 were of the same order of magnitude (a constraint was applied to the value of r_2 so that $r_2 = r_1 \mp 0.2$). The methodology was applied to each of the 101 selected models, and we recorded, for each KS index, the number of models with validated rank correlation tests (i.e. satisfying the three conditions specified above). We also ran, for comparison, the same tests without applying any constraint on the order of magnitude of the correlation coefficients.

4.2.3. Selection of the most promising KS index

4.2.3.1 Implementation of a classification tree

We implemented a classification tree (Figure 4.1a), as an alternative to the KS indices for the identification of keystone species among the functional groups of each modeled ecosystem. The classification was based on two (log-transformed) parameters: the trophic impact (in squared values) (ε_i^2) and biomass (B_i) of each group *i*. Four main categories were discriminated: 'Keystone' (corresponding to groups with high impact and low biomass), 'Low Impact – Low Biomass', 'Low Impact – High Biomass', 'High Impact – High Biomass', and 'Intermediate' (corresponding to groups belonging to none of the previous categories). Quartiles values of both ε_i^2 and B_i parameters, over all living groups in each model, were set as thresholds to identify groups belonging to each category. The third quartiles (Q_3) were set as lower thresholds for delimiting groups with high ε_i^2 and B_i , while the first quartiles (Q_1) as upper thresholds for groups with low ε_i^2 and B_i . The other thresholds were defined by the minimum (*min*) or maximum (max) values of ε_i^2 and B_i recorded for each modeled ecosystem. Then, among the identified keystone species, we separated the ones with a high trophic level from the others. Thus, a supplementary parameter, the trophic level (TL_i) of each group, was used to discriminate the Keystone groups in two sub-categories: 'Low TL Keystone' (whose *TL* was lower than the third quartile values of *TL*), and 'High TL Keystone' (whose *TL* was equal to or higher than Q_{3TL}). The classification tree was applied to each of the 101 selected models, and a scatter plot representing the classification of each group was produced for each model (Figure 4.1b). The categories identified with the classification tree were recorded for all groups and all models.

4.2.3.2 Comparison between keystone groups identified with the KS indices and with the classification tree

The keystone groups identified with the classification tree were compared to the ones identified with the KS indices. Precisely, for each of the 101 selected models and each of the KS index, we compared the group with the highest value of keystoneness with the KS index to the groups categorized as (Low TL or High TL) Keystone with the classification tree. If the group with the highest KS index value was classified in the (Low TL or High TL) Keystone categories of the classification tree, then the identified keystone group was considered as validated, for the selected model. The methodology was applied to each of the 101 selected models, and we recorded, for each KS index, the number of models with validated keystone group.

In addition, once the most promising KS index was selected (see Section 4.2.3.3), the groups identified as keystone (i.e. with the highest value of keystoneness) with the selected index were compared across the 101 selected models. Then, we compared the most frequently identified groups with the selected index and with the classification tree. Since the 101 models followed different rules for naming their respective functional groups, the names of the keystone groups identified with the selected index were standardized before comparison. Groups were renamed (and sometimes aggregated) using generic group names, based on their original designations. The same standardization method was applied to the groups classified as Low TL or High TL Keystone with the classification tree.

4.2.3.3 Allocation of overall statuses to the KS indices

The conclusions from the rank correlation tests and the classification tree were summarized and confronted by allocating different statuses to each pair of 'Ecopath model - KS index' (Figure 4.2). The results obtained from the status allocation were used for the selection of the most promising of the 12 KS indices applied in the analysis. Statuses were allocated according pre-defined rules and following three steps: (1) if the KS index was validated (correlated positively with IC and BC, and with correlation coefficients of the same order of magnitude), then the result from the rank correlation tests was positive, negative if not; (2) if the identified keystone group was validated (group of highest keystoneness with the KS index classified in the Keystone categories of the classification tree), then the result from the classification tree was positive, negative if not; (3) if results from both steps 1 and 2 were positive (respectively negative), then the status was labeled as 'True Positive', (respectively 'True Negative'), but if step 1 was positive and step 2 negative (respectively step 1 negative and step 2 positive), then the status was labeled as 'False Positive' (respectively 'False Negative'). Thus, there were four alternative statuses possible for each 'Ecopath model – KS index' pair: True Positive, False Positive, False Negative and True Negative. In other words, when the result from the rank correlation tests (step 1) was positive, the status was labeled as 'positive', 'negative' if not, and when the result from the classification tree (step 2) was in agreement with step 1, the status was also labeled as 'True', 'False' if not. For some models, none of the functional groups was classified in the Keystone categories of the classification tree, so that the identified keystone group could not be confirmed or unfirmed (step 2). Thus, a supplementary status was defined for these models, and labeled as 'No Keystone'. The status allocation was performed for each of the 101 selected models, and the number of models associated with each status (True Positive, False Positive, False Negative, True Negative and No Keystone) was recorded, for each KS index. The 'Overall Status', obtained for each KS index over all models, corresponded to the status allocated to the majority of models.

4.2.4. Application to a case study

A case study was chosen to which both the classification tree described above and the selected KS index were applied. We chose the Ecopath model representing the Prince William Sound, a nearly enclosed embayment located in the northern Gulf of Alaska, for the time period between 1994 and 1996, and covering an area of about 9,000 km², with a mean depth of 300 m (Okey and Pauly 1999). This Ecopath model was originally built to better understand the structure and functioning of the food web, based on the information provided by a panel of 35 experts (Okey and Pauly 1999). See Appendix B for graphical representations of the Prince William Sound (1994-1996) food web.

4.3. **Results**

4.3.1. Pool of selected Ecopath models

After applying the scoring method, we obtained a selection of 101 Ecopath models, whose final scores ranged from 2 to 6. Analyses of keystone species were previously performed on 23 of the 101 models. In fact, most models were included in the meta-analysis introducing the KS#2 index (Libralato et al. 2006), or were applied the latter index by their authors, while four models were applied alternative original methods proposed by the modelers (Aydin et al. 2002, Kitchell et al. 2002, Okey et al. 2004). The selection comprises 13 models representing MPAs, and only 5 of them are fully unexploited ecosystems (no fishing fleet defined). However, the No Keystone status was allocated to the majority of the MPA models. About a third (39) of the selected models focuses on a (group of) species of particular interest. The selection includes 81 sibling models, but only 2 overlapping models. In fact, only 48 of the sibling models are suitable for comparative analyses, since some models did not have their corresponding siblings selected, others had different species aggregations between siblings, and some siblings were associated to the No Keystone status. See Appendix C (Table C1) for the detailed results of the scoring method for each selected model.

Most of the 101 selected models seem to be good quality models in terms of data. A large proportion of the models (78) provide detailed information on species aggregation into functional groups. Approximately one third of the selected models do not have any biomass input data computed by Ecopath, and the proportions of estimated biomass is lower than 25% for the second third, and lower than 75% for the last third (up to 95% for only one model). Besides, the selection comprises 43 Ecopath model fitted to time-series. See Appendix C (Tables C2 and C3) for the detailed metadata and references of each of the 101 selected models.

The 101 selected models represent a wide variety of marine ecosystems. Continental shelf (less than 200 m deep) is the most represented type of ecosystem with 41 models. Six other types are represented in smaller proportions: ocean (more than 200 m deep, 19 models), upwelling (16), channel or strait (10), bay or fjord (7), coral reef (7), and coastal lagoon (1). Most modeled ecosystems are located in temperate or tropical zones (58 and 36 models, respectively), and few in polar zones (7). About two thirds of the selected models represent ecosystems over a time period of one year, and the last third covers time periods lasting from 2 to 11 years (up to 40 years for one model). About half of the models describe ecosystems in the recent past (49 models for the 1990s-2000s), while the other half describe ecosystems in more ancient times (26 for the 1970s-1980s, 18 for the 1950s-1960s, and 8 for periods before 1950). The spatial extent of the selected models varies from 2.48 to more than 18,000,000 km², but most models cover an area smaller than 500,000 km^2 (Figure 4.3a). Among the selected models, ecosystems of the ocean and continental shelf types have the wider ranges of spatial extent, whereas the ocean and upwelling types cover the largest areas, followed by continental shelf and channel or strait (Figure 4.3a). Coral reef ecosystems have the wider range and highest values of total biomass (Figure 4.3b), whereas upwelling ecosystems have the wider range of total catch, followed by bay or fjord and channel or strait (Figure 4.3c). The number of living groups in the 101 selected models ranges from 6 to 96, with most models comprising 20 to 40 groups (Figure 4.4a). The number of fishing fleets varies from 0 to 19, with 14 models without fleet, and most models including 1 to 5 fleets (Figure 4.4b). Among models with defined fishing fleets, the mean trophic level of the catch ranges from 1.02 to 4.52, and is comprised between 3 and 3.5 for most models (Figure 4.4c).

4.3.2. Balance in the contributions of IC and BC to the KS indices

The comparison between the groups ordered by keystoneness and by trophic impact and biomass, applied to the 101 Ecopath models and for each KS index, shows that three of the KS indices out of the 12 seem to be balanced: KS_3 , KS_7 , and KS_{12} (Table 4.2). For these three indices, the spreading of the models is comparable between the three matching categories, so that none of the categories is associated to the majority of models (51 or more) and no Overall Match is determined. Thus, for these three indices, the group with the highest keystoneness value may also have one of the three highest trophic impact values, or one of the three lowest biomass values, or none of the previous, with similar probabilities. Nonetheless, we note that the number of models is higher (and close to the majority) in the Match Impact category for the KS_3 index. In addition, the comparison shows that both KS_1 and KS_2 indices (directly adapted from the literature) are unbalanced. KS_1 has a significantly higher number of models (91) in the Match Impact category, meaning that this index tends to identify keystone groups mainly based on their (high) trophic impact. In contrast, KS_2 has a significantly higher number (81) of models in the Match Biomass category, so that it would identify keystone groups primarily based on their (low) biomass. The Overall Match of the other KS indices corresponds to, either Match Impact, or Match Biomass, determined with a more or less substantial majority of models.

The rank correlation tests are validated for a majority of the 101 models for only one of the 12 KS indices: KS_3 , with 75 models with validated tests (Table 4.3). Both KS_1 and KS_2 indices show significantly lower numbers of models with validated rank correlation tests, with respectively 40 and 12 models. The other KS indices have less than 10 models with validated tests (apart from KS_6 with 44 models). Thus, the results from the tests demonstrate a better balance between IC and BC components for the KS_3 index, for which high keystoneness values seem to correlate, with the same order of magnitude, to high trophic impact and low biomass values. When the constraint on the magnitude order of the correlation coefficients is released, the conclusions from the tests are not changed: KS_3 appears as the most balanced index. The number of models with validated (unconstrained) tests increases for most of the KS indices (apart from KS_8 and KS_9 , for which it remains equal to zero), yet the KS_3 index still has the highest number, with 99 models. When unconstrained, the rank correlation tests are validated for a majority of models with four other indices, including KS_1 and KS_2 , with respectively 95 and 52 models.

4.3.3. Selection of the most promising KS index

Based on the classification tree (Figure 4.1), we could confirm or not the keystone groups identified with each of the 12 KS indices, for each of the 101 models (Table 4.3). The number of models with a validated keystone group (i.e. belonging to the Keystone categories of the classification tree) ranges from 15 to 59, over all KS indices. The KS_3 index shows one of the highest scores (with 48 models), whereas the KS_1 and KS_2 indices show lower scores (with 15 and 34 models, respectively).

Then, by confronting the results from the rank correlation tests and the classification tree, we could allocate alternative statuses to each of the 101 models, for each of the 12 KS indices (Figure 4.2). Since 33 models were allocated a No Keystone status (no functional groups in these models was categorized as Keystone with the classification tree), the majority was reduced to 35 models to determine the Overall Status of each KS index. The outcomes from the status allocation corroborate the selection of the KS_3 index as the most promising one. Indeed, KS_3 is the only one index associated with a True Positive Overall Status (with 40 True Positive models), meaning that results from the tests (step 1) and the classification tree (step 2) are both positive for a majority of models (Table 4.3). Two indices, KS_5 and KS_9 , are allocated a True Negative Overall Status (with 46 and 53 True Negative models, respectively), traducing negative conclusions from both steps 1 and 2. For three of the KS indices $(KS_1, KS_2 \text{ and } KS_6)$, none of the statuses is associated with the majority of models, so that no Overall Status is determined for these indices. Nonetheless, we note that the number of True Negative, respectively False Negative, models is close to the majority for KS_1 , respectively KS_2 (with 32 models in each case). The remaining KS indices are allocated a False Negative Overall Status, indicating a negative result from the tests while the result from the classification tree is positive.

4.3.4. Identification of potential keystone groups with the selected KS index and the classification tree

The selected KS_3 index was applied to the 101 selected Ecopath models, so that the results from the whole analysis may be analyzed in terms of species (or groups). We compared, across the 101 selected models, the most frequently identified keystone groups with the KS_3

index (i.e. with the highest value of keystoneness) and with the classification tree (i.e. belonging to the High TL or Low TL Keystone categories).

Groups are labeled using 12 generic group names, to standardize their heterogeneous original designations (Figure 4.5a and Figure 4.5b). Fish groups are distinguished into 4 groups: 'Elasmobranchii' (including groups of sharks and rays), 'Gadiformes' (cod and hake groups), 'Scombroidei' (tunas, billfishes, and barracudas groups), and 'Fishes' (all the other groups of fishes). We note that the latter group of fish corresponds to a relatively wide range of species, aggregating groups of both large pelagic and small demersal, because they all have low occurrences as identified keystone groups. Mammals groups are discriminated between: 'Odontoceti' (comprising groups of dolphins and orcas, as well as unspecified toothed whales), 'Pinnipedia' (seals, sea lions, and walruses groups), and 'Mammals' (baleen whales groups, and unspecified groups of cetaceans and mammals). The other groups differentiate 'Seabirds' (all groups of birds), from 'Invertebrates' (comprising crustaceans, cephalopods and unspecified invertebrates). The 'Zooplankton', 'Producers', and 'All Fleets' groups are unchanged from their original designations.

Overall, the groups identified as keystone species with the highest occurrences across models correspond to cartilaginous fishes and toothed whales (Figure 4.5a and Figure 4.5b). The most frequently identified groups with the KS_3 index, across the 101 models, are: Elasmobranchii, All Fleets, Fishes, and Odontoceti (Figure 4.6a). In comparison, the most frequently identified groups with the classification tree, across the 101 models, are: Elasmobranchii, Pinnipedia, Odontoceti, and Fishes (Figure 4.6b). With the classification tree, the identified keystone groups may be discriminated with their trophic level (Figure 4.6b). Thus, Odontoceti scores higher than Pinnipedia when considering High TL Keystone only. Besides, All Fleets are Low TL Keystone, as well as a substantial proportion of the Seabirds and Fishes. The keystone groups identified with the KS_3 index may be discriminated based on the status of the models (Figure 4.6a). Thus, the most frequently identified groups associated to a True Positive status are: Elasmobranchii and Odontoceti. In contrast, the most frequently identified groups associated to a No Keystone status are All Fleets and Fishes. Finally, the High TL Keystone groups, such as Scombroidei or Gadiformes, correspond to a True Positive status. See Appendix C (Table C4) for the detailed results obtained with the selected KS_3 index, for each model.

4.3.5. Case study of the Prince William Sound (1994-1996) food web

With the selected KS_3 index, the Ecopath model of the Prince William Sound (1994-1996) show positive results from the rank correlation tests. Also, the same groups are identified as potential keystone species, both with the classification tree (Figure 4.6) and the selected KS_3 index (Figure 4.7a), in the Prince William Sound (1994-1996) food web. Transient orcas (group number 1) are classified as High TL Keystone and have the highest value of keystoneness with the KS_3 index. Avian predators (group number 15, mainly representing bald eagle) are categorized as Low TL Keystone and have the second highest keystoneness value. Thus, the status of the selected KS_3 index applied to the case study model is True Positive. In contrast, with the KS_1 and KS_2 indices directly adapted from the literature, results from the classification tree are in disagreement with results from the rank correlation tests. More precisely, the groups having the highest values of keystoneness with the KS_1 index belong to the High Impact – High Biomass category (Figure 4.7b). With the KS_2 index, although transient orcas and avian predators have the two highest keystoneness values, the correlation tests were not validated, seeing that the groups classified as Low Impact – Low Biomass have high keystoneness (Figure 4.7c).

4.4. Discussion

4.4.1. A balanced index of keystoneness for marine food webs

In this study, we derived a functional index estimating species keystoneness from a metaanalysis on a selection of 101 Ecopath models. The selection of models was representative of the variety of marine ecosystems worldwide. Also, most models were of good quality in terms of data. The Ecopath-based approach enabled us to use trophic impact and biomass as measurable species traits, and to propose ecosystem-specific thresholds of minimum trophic impact and maximum biomass for species to be keystone. In each modeled food web, species were ranked according to their keystoneness estimates, so that the potential keystone species could be quantitatively identified. The new index of keystoneness proposed in our study (the KS_3 index) was obtained by multiplying the IC_L impact component (adapted from Libralato et al. 2006) by the BC_0 biomass component (based on descending ranking, so that high biomass corresponds to low BC). The usage of ranking in the biomass component enabled us to prevent "inflating uncertainty and errors in the index because measures for rare species are divided by small numbers" (Cottee-Jones and Whittaker 2012). The KS_3 index was selected by confronting the results from two statistical methods: (i) Spearman's rank correlation tests (step 1); and (ii) a classification tree (step 2). The selected index corresponded to the KS index with the highest number of models for which results from both steps 1 and 2 were positive.

The standardized Ecopath approach allowed for a comparison of the keystone groups identified across models. The generic groups of species with the highest occurrences across models were cartilaginous fishes and toothed whales, over all the 101 selected models. These species corresponded to the definition of keystone predator applied in this study. As for the case study model, the identification of a toothed whales species (transient orcas) as a potential keystone group was consistent with empirical knowledge on the modeled ecosystem. Although sea otters are known as an historical example of keystone species in kelp forest ecosystems (Estes and Palmisano 1974), transient orcas were identified as keystone species in the Ecopath model of the Prince William Sound (1994-1996). Alaskan transient orcas were observed to be partially feeding on sea otters, themselves mainly feeding on clams but rarely on sea urchins (Estes et al. 1998, Okey and Pauly 1999). Thus, the keystoneness of sea otters was reduced in the Prince William Sound food web, due to both the predation pressure from transient orcas (Estes et al. 1998), and the low abundance of grazers such as sea urchins (Paine 1980).

In this study, we established that the selected index (KS_3) seemed to be more balanced than the ones previously proposed in the literature and implemented in EwE $(KS_1 \text{ and } KS_2)$. Both KS_1 and KS_2 indices were applied to several modeled food webs, representing various types of marine ecosystems (e.g., Libralato et al. 2006, Coll and Libralato 2012, Coll et al. 2013). As for the six models selected in this study to which the latter indices were applied, the results from the KS_1 index were not convincing for four of the models (Coll et al. 2007, Tsagarakis et al. 2010, Valls et al. 2012, Tecchio et al. 2013), and inconsistent results were obtained when both KS_1 and KS_2 indices were used. In this study, we confirmed that both KS_1 and KS_2 indices fail attributing high keystoneness to groups having both low biomass and high trophic impact. The KS_1 index frequently attributed high keystoneness to functional groups with high biomass, provided their trophic impact was high. Such groups would rather correspond to abundant species (Coll and Libralato 2012). In contrast, the KS_2 index often gave high values for functional groups with low biomass, even though these groups had low trophic impact. Such groups would rather be categorized as rare species (Libralato et al. 2006, Coll et al. 2013). The KS_3 index proposed in this study was demonstrated to have more balanced contributions between its trophic impact and biomass components in its estimation of species keystoneness. Therefore, the new index may be used to identify keystone species in marine food webs, without over-representing abundant or rare species.

4.4.2. Methodological considerations on the derived functional KS index

The MTI analysis, like the Ecopath model, only gives a snapshot of the trophic web at one point in time, and should not be used for drawing conclusions on the consequences of changes in biomass over time. For instance, a decrease in the biomass of a predator might lead to an increase in the biomass of its prey in the short term. In the longer term, it might also result in higher biomasses of other predators, or changes in the predator's diet facing reduced prey abundance, but these cumulative effects cannot be predicted from the MTI analysis (Christensen and Walters 2004). However, the (positive or negative) m_{ij} corresponds, for each pair of groups (i, j) in the modeled food web, to the relative change (increase or decrease) in the biomass of the impacted group j, caused by a slight increase in biomass of the impacting groups i (Libralato et al. 2006).

The main criticism about Ecopath-based approaches, especially when looking at keystone species, deals with the species aggregation into functional groups. Aggregating species is required to obtain smaller and simpler food webs, easier to analyze. A few methods of aggregation are commonly used, yet there are no systematic aggregation rules, which potentially introduce taxonomic bias (Jordán 2009). Other than mass-balance food web models, alternative methods to identify ecologically important species, such as keystone species, are based on Ecological Network Analysis (ENA). ENA-based approaches are used to derive quantitative structural indices describing species position in complex networks of interspecific interactions (e.g., Estrada 2007, Jordán 2009, Jordán et al. 2009). ENA methods consist in topological studies applied in ecology to characterize the positional importance of species in communities, by

considering the number of trophic links between species, but not necessarily the strength of the links (Jordán 2009). Such methods were first applied to binary networks only (e.g., Jordán et al. 2003), and then adapted to weighted networks (e.g., Scotti et al. 2007, Jordán et al. 2008), since weighted structural indices were demonstrated to best correlate with functional indices from EwE-based methods (Jordán et al. 2008). Alike food web models, ecological networks are aggregated to some extent, seeing that all species are directly or indirectly interconnected in the food web (Jordán 2009). Besides, ENA studies are based on the Lotka-Volterra assumption of uniform and random distribution of interactions between species (e.g., Christianou and Ebenman 2005). Yet, the latter assumption was proven to be unrealistic, compared to the foraging arena theory implemented in EwE models (Walters and Martell 2004, Walters and Christensen 2007, Ahrens et al. 2012). Finally, community structure and dynamics were shown to be correlated in EwE studies (Libralato et al. 2006). Likewise, another challenge for ENA-based approaches is to understand species importance, not only in terms of network position, but also regarding network dynamics (Jordán 2009).

4.4.3. Perspectives for future directions in keystoneness analyses

The major challenge in the quest for keystone species is the estimation of the time and space required to assess potential keystone effects (Paine 1995, Power and Mills 1995). Thus, the temporal and spatial scales considered are determinant to the identification of keystone species. Although static patterns differ from dynamic processes (Paine 1980, Arponen 2012), it was verified that the keystoneness of species may be inferred without performing time-dynamic analyses (Libralato et al. 2006). Thus, in this study, we chose to compare Ecopath models of past and present ecosystem states, rather than using Ecosim simulations. Such approach was previously applied to a selection of models representing upwelling ecosystems at different time periods (Libralato et al. 2006), or used to analyze the effects of the establishment of an MPA (Coll et al. 2009, Eddy et al. 2014). Here, we preferentially selected models representing the same ecosystem at different temporal periods (sibling models) or spatial scales (overlapping models), in order to integrate temporal and spatial variability. We ended up with very few (only 2) overlapping models, so that we could not analyze the influence of spatial scale. In contrast, our selection of Ecopath models comprised a large number of sibling models, which were used to
explore context-dependency issues a little further. We used the selected sibling models to compare the changes in identified keystone groups over time in the same ecosystem. However, no consistent pattern could be identified across our selection of sibling models. A more in-depth analysis would be required to fully understand the interacting factors affecting species keystoneness over time.

Human-induced variability may be a factor of potential influence on species keystoneness. Anthropogenic impacts may lead to the loss of keystone species (first becoming rare, and then disappearing) and the community architecture they maintained, leaving an altered ecosystem where species are less likely to play keystone roles (Paine 1995). On the contrary, Power et al. (1996) argued that loss of species diversity may lead to the remaining species taking on keystone roles. Using the KS_1 and KS_2 indices, several authors demonstrated that ecosystems highly affected by fishing impact had less prevalence of keystone species, whose role was modified with increased fishing pressure. As an example in the Mediterranean Sea, the proportion of keystone species in fully exploited ecosystems was shown to be less prevalent than in protected (or slightly exploited) ecosystems, while the proportion of abundant species were comparable across ecosystems (Coll and Libralato 2012). A similar pattern was observed globally, in a study considering coastal ecosystems from all over the world ocean (Heymans et al. 2012). Keystone species in non-exploited marine ecosystems may become rare when overexploitation occurs, such as cetaceans in the Mediterranean Sea (Coll et al. 2009), or groupers in the Galapagos (Okey et al. 2004). Similarly, the keystone species status of lobsters in New Zealand was shown to be impacted by fisheries (Eddy et al. 2014). Consequently, human activities could result in large-scale removals of potential keystone species, without any record of the ecosystem state before the uncontrolled removals (Power et al. 1996). Human-induced climate change may be determinant to the keystone role of species as well (Harley 2011). Through the same mechanisms as in natural variability, human-induced variability may lead to competitive balance shifts and predator removals, and thus alter species interactions (Poloczanska et al. 2008).

The fishing fleets defined in the selected Ecopath models were included as human predators in our analysis, so as to consider potentially significant anthropogenic (fishing) impacts on keystone species. The All Fleets group appeared as a frequently identified keystone group with the selected index (Figure 4.5a), which could suggest a significant effect of fishing on

keystone species in the corresponding modeled food webs. However, the keystoneness of the All Fleets group was not confirmed with the classification tree, since most corresponding models were allocated a No Keystone status (Figure 4.5a). We observed that the Overall Match and Overall Status of the different KS indices were not modified by the inclusion of fishing fleets in the calculation of the mixed trophic impacts. Nonetheless, the sensitivity of the identified keystone group to the addition of the All Fleets group in the analysis varied among the different KS indices. Ideally, an index of keystoneness would consider context-dependency aspects and identify keystone species differently depending on the status of the ecosystem. Alternatively, a suite of complementary indices, each best adapted to a specific level of exploitation, could be developed and applied according to the situation. So, further analyses could explore the sensitivity of the proposed KS index to context-dependency, by comparing the changes in identified keystone species with the changes in fishing pressure in the modeled food web. In the literature, sensitivity analyses on matrix models representing ecological succession were notably used to quantify the relative importance of species interactions to community composition and proposed as a method to identify keystone species (Tanner et al. 1994). In addition, we could investigate the robustness of the proposed KS index to uncertainty and possible model construction errors. Structural indices for binary food webs, such as the mixed trophic impact, were demonstrated to be robust to uncertainty (Fedor and Vasas 2009), so that the equivalent functional indices for weighted food webs, used in our approach, may be assumed to be robust as well. Yet, the development of a measure of robustness for functional indices of keystoneness, similar to the one applied to structural indices, would constitute interesting questions for future studies.

4.4.4. Toward an index of keystoneness applicable to biodiversity conservation

In this study, we developed an operational methodology, directly applicable to marine ecosystems, and possibly adaptable to other types of systems (freshwater or terrestrial). Food web dynamics and keystone species may respond differently, depending on the type of ecosystem (Bond 2001, Link 2002a). The response to species introduction or removal is known to be generally slow in natural ecosystems, but the time scale is thought to be shorter in aquatic ecosystems, especially lakes, than in terrestrial ones (Bond 1994, Power et al. 1996, Bond 2001).

Marine food webs differ from other types of food web by their higher connectivity, due to large ontogenetic changes in size and diet of marine species, which are opportunistic feeders in an open foraging range (Link 2002a). Therefore, the detection of keystone mechanisms might be eased in freshwater or terrestrial food webs.

Conserving biodiversity is often a compromise between protecting species, areas, or processes (Simberloff 1998). Among the critical ecological processes maintaining whole communities, some are driven by critical species, which thus have to be identified and used in the "conservation biologist's toolbox" (Power et al. 1996). Critical species play an important ecological function, performed by few other species in the ecosystem, such as keystone species which maintain the food web structure of their community (Perry 2010). Thus, identifying and protecting critical species may be the only long-term solution to preserve a "working ecosystem" rather than a collection of charismatic species" (Jordán 2009, Perry 2010). In this study, we focused on the keystone species category, yet other categories of critical species may be identified with the classification tree. Indeed, species belonging to the High Impact - High Biomass category may correspond to critical food resources in the food web. On the contrary, the Low Impact – Low Biomass category may include some rare species, potentially endangered or ecologically extinct. Lastly, the fourth category of Low Impact - High Biomass species may represent critical habitat species in the ecosystem. In practice, analyzing functional roles in species assemblages is determinant to setting conservation priorities and defining restoration programs (McClanahan 2000, Clemente et al. 2010). The identification of functionally important species, such as keystone species, not only helps developing effective conservation strategies for species-level prioritization, but also better understanding of ecosystem functioning and processes (Jordán 2009, Clemente et al. 2010). Moving toward a fully operational and widely applicable index of species keystoneness would thus constitute one step further in biodiversity conservation.

Table 4.1. Equations of the 12 indices of keystoneness (KS), obtained by combining each impact components (IC) with each biomass components (BC). ICs were calculated using a measure of trophic impact (ε_i) (Equation 4.2), and BCs using a measure of biomass (B_i) (Equation 4.3). The components adapted from the literature were called with a subscript capital letters: IC_L and BC_L (Libralato et al. 2006), and BC_P (Power et al. 1996). The other components were called using subscript numbers, with a zero for the components using ranks: IC_0 and BC_0 . The abbreviations 'arank' and 'drank' designate the rank of the variable, with a ranking in ascending and descending order, respectively.

KS Indices	Impact Components	Biomass Components
$KS_1 = IC_L \times BC_L$	$IC_L = \varepsilon_i$	$BC_L = 1 - p_i$
$KS_2 = IC_L \times BC_P$		$BC_P = 1/p_i$
$KS_3 = IC_L \times BC_0$		$BC_0 = drank(B_i)$
$KS_4 = IC_L \times BC_1$		$BC_1 = 1/\sqrt{B_i}$
$KS_5 = IC_0 \times BC_L$	$IC_0 = arank(\varepsilon_i)$	$BC_L = 1 - p_i$
$KS_6 = IC_0 \times BC_P$		$BC_P = 1/p_i$
$KS_7 = IC_0 \times BC_0$		$BC_0 = drank(B_i)$
$KS_8 = IC_0 \times BC_1$		$BC_1 = 1/\sqrt{B_i}$
$KS_9 = IC_1 \times BC_L$	$IC_1 = \varepsilon_i^2$	$BC_L = 1 - p_i$
$KS_{10} = IC_1 \times BC_P$		$BC_P = 1/p_i$
$KS_{11} = IC_1 \times BC_0$		$BC_0 = drank(B_i)$
$KS_{12} = IC_1 \times BC_1$		$BC_1 = 1/\sqrt{B_i}$
Where	$\varepsilon_i = \sqrt{\sum_{j \neq i} m_{ij}^2}$	$p_i = \frac{B_i}{\sum_{k=1}^n B_k}$

Table 4.2. Results from the comparison between groups ordered by keystoneness, and by trophic impact or biomass, for each KS index, over all selected models. Both indices adapted from the literature (KS_1 and KS_2) are highlighted in gray, and the selected index (KS_3) is in bold. The number of models whose group with the highest keystoneness matched one of the three groups with highest trophic impact (ε_i), respectively with the lowest biomass (B_i), is shown in the first column (*Match Impact*), respectively in the second column (*Match Biomass*). The number of models for which the group with the highest keystoneness value matched none of the three groups with, either the highest trophic impact, or the lowest biomass, is shown in the third column (*No Match*). In the last column (*Overall Match*), results are expressed as an overall match for each KS index over all models, corresponding to the matching category of the majority of models (i.e. 51 models or more, for a total of 101 models) for the particular index. Note: "_" indicates no majority. See Table 4.1 for detailed equations of each KS index.

KS Index	Match Impact	Match Biomass	No Match	Overall Match
KS_1	91	10	0	Match Impact
KS_2	5	81	15	Match Biomass
KS ₃	50	28	23	_
KS_4	25	54	22	Match Biomass
KS_5	86	12	3	Match Impact
KS ₆	0	94	7	Match Biomass
KS_7	32	35	34	_
KS_8	11	70	20	Match Biomass
KS ₉	91	10	0	Match Impact
KS_{10}	25	54	22	Match Biomass
KS_{11}	71	20	10	Match Impact
KS_{12}	46	39	16	_

Table 4.3. Results from the rank correlation tests (column 2), the classification tree (column 3 – see Figure 4.1) and the status allocation (columns 4 to 8 – see Figure 4.2), for each KS index. Both indices adapted from the literature (KS_1 and KS_2) are highlighted in gray, and the selected index (KS_3) is in bold. Values correspond to the number of models with: validated rank correlation tests (*Correlation*); whose keystone group identified with KS index is categorized as Keystone with classification tree (KS *Category*); and whose associated status corresponds to each of the possible statuses (*True Positive, False Positive, False Negative* and *True Negative*). In column 2 (*Correlation*), the first sub-column gives the results with a constraint applied on the correlation coefficients, and the second sub-column (values shown in parentheses) gives the results with no constraint applied. In column 8 (*Overall Status*), results are expressed as an overall status for each KS index, corresponding to the status of the majority of models (i.e. 35 models or more, since 33 models over the 101 models in total were allocated a No Keystone status), for the particular index. Note: "_" indicates no majority. See Table 4.1 for detailed equations of each KS index.

KS Index	Correlation		KS Category	True Positive	False Positive	False Negative	True Negative	Overall Status
KS_1	40	(95)	15	7	21	8	32	_
KS_2	12	(52)	34	6	5	32	25	_
KS ₃	75	(99)	48	40	12	14	2	True Positive
KS_4	0	(0)	50	0	0	55	13	False Negative
KS ₅	0	(0)	22	0	0	22	46	True Negative
KS ₆	44	(50)	22	17	24	9	18	_
KS_7	9	(14)	59	7	1	59	1	False Negative
KS_8	0	(51)	43	0	0	48	20	False Negative
KS ₉	0	(8)	15	0	0	15	53	True Negative
KS_{10}	1	(1)	50	0	1	55	12	False Negative
KS_{11}	2	(8)	35	1	0	37	30	False Negative
KS ₁₂	3	(7)	47	2	1	51	14	False Negative



Figure 4.1. Identification of keystone species with a classification tree. (a) Classification tree for the identification of keystone species among the functional groups of each modeled ecosystem. The classification is based on two (log-transformed) parameters: the biomass (B_i) and trophic impact (in squared values) (ε_i^2) of each group. Groups are classified using the first quartile (Q_1) and third quartile (Q_3) values of the parameters over all living groups in each model, as lower and upper thresholds. Four main categories are discriminated: Keystone (i.e. groups with high impact and low biomass), Low Impact – Low Biomass, Low Impact – High Biomass, High Impact – High Biomass, and Intermediate. The Keystone category is subdivided into two sub-categories: Low TL Keystone and High TL Keystone, by comparing the trophic level (TL_i) of the group to the third quartile values of TL. The diamond-shaped boxes represent yes/no questions, and the rectangle-shaped boxes the categories identified after answering the questions. (b) Simplified graphical representation of the classification tree on a scatter plot, with the biomass (B_i) on the x-axis, and the trophic impact (in squared values) (ε_i^2) on the y-axis, both in log values. The upper-left box represents the area where the (Low TL and High TL) Keystone groups are located, the upper-right box where the High Impact – High Biomass groups are, the lower-left box where the Low Impact – Low Biomass groups are, and the lower-right one where Low Impact – High Biomass groups are. Each category box is defined based on the classification tree, using the minimum (min), maximum (max), first quartiles (Q_1) and third quartiles (Q_3) values (see Figure 4.1a). Intermediate groups are spread on the rest of the plotting area (shaded in gray).



Figure 4.2. Rules for status allocation to each pair of 'Ecopath model – KS index'. The statuses were allocated in three steps: (1) if the KS index was validated, then the result from the rank correlation tests was positive, negative if not; (2) if the identified keystone group was validated, then the result from the classification tree was positive, negative if not; (3) if results from step 1 and 2 were both positive (respectively both negative), then the status was labeled as 'True Positive', (respectively 'True Negative'), but if step 1 was positive and step 2 negative (respectively step 1 negative and step 2 positive), then the status was labeled as 'False Positive' (respectively 'False Negative'). Four alternative statuses are possible for each 'Ecopath model – KS index' pair: True Positive, False Positive, False Negative and True Negative. A positive result for step 1 means that the KS index was validated for the selected model, because it was correlated positively with IC and BC, with correlation coefficients of the same order of magnitude. A positive result for step 2 means that the identified keystone group was validated for the selected model, since the group of highest keystoneness with the KS index was categorized as Keystone with the classification tree.



Figure 4.3. Boxplots of (a) spatial extent (*Area*, thousands of km²), (b) total biomass (B_{tot} , t·km²), and (c) total catch (Y_{tot} , t·km⁻²·year⁻¹), for all selected Ecopath models, categorized by type of modeled ecosystem: bay / fjord (B/F), channel / strait (C/S), coastal lagoon (CL), continental shelf (CS), coral reef (CR), ocean (Oc), or upwelling (Up). The horizontal line in each box represents the median number of models.



Figure 4.4. Boxplots of (a) number of living groups, (b) number of fishing fleets, and (c) mean trophic level of the catch (TL_Y) , for all selected Ecopath models. The horizontal line in each box represents the median number of models.



Figure 4.5. Bar plots of the groups identified as keystone with (a) the selected KS_3 index, and (b) the classification tree. Values are expressed in number of models, over the 101 selected Ecopath models. Based on their original names in each model, the identified keystone groups are aggregated into 12 broader groups: All Fleets, Elasmobranchii, Fishes, Gadiformes, Invertebrates, Mammals, Odontoceti, Pinnipedia, Producers, Scombroidei, Birds, and Zooplankton. With the KS_3 index, the identified keystone groups may be discriminated based on the status of the model: True Positive (*TP*), False Positive or False Negative or True Negative (*FP / FN / TN*), and No Keystone (*NKS*). With the classification tree, the identified keystone groups may be classified as, either High TL Keystone (*High TL KS*), or Low TL Keystone (*Low TL KS*).



Figure 4.6. Application of the classification tree (see Figure 4.1) to the Prince William Sound (1994-1996) food web (Okey and Pauly 1999). The scatter plot shows the biomass (B_i) on the x-axis, and the trophic impact (in squared values) (ε_i^2) on the y-axis, both in log values. Each dot is a functional group in the model, identified with a group number and a group name (indicated in the legend). Groups belonging to each category are displayed in the same color as the corresponding category box: Keystone groups in pink (upper-left box), High Impact – High Biomass groups in orange (upper-right box), Low Impact – Low Biomass groups in green (lower-left box), and Low Impact – High Biomass groups in blue (lower-right box). Keystone groups are subdivided in two categories: Low TL Keystone in dark pink and High TL Keystone in pink. The All Fleets group, for which B_i was approximated with the total catch (Y_{tot}) , corresponds to the aggregation of all the fishing fleets defined in the model.



Figure 4.7. Application of the (a) KS_3 , (b) KS_1 , and (c) KS_2 indices (see Table 4.1) to the Prince William Sound (1994-1996) food web (Okey and Pauly 1999). Each scatter plot shows the rank of the functional groups, based on its index of keystoneness in ascending order (keystone species have high ranks), on the x-axis, and the trophic level (TL_i) of the functional groups on the y-axis. Each dot is a functional group in the model, identified with a group number and a group name (indicated in the legend). The All Fleets group corresponds to the aggregation of all the fishing fleets defined in the model. Groups are displayed in the color of the category they were associated to on the classification tree (see Figure 4.6).

5. Selectivity of fish feeding: potentials, challenges and recommendations

5.1. Introduction

Diet compositions for fish species are usually derived from stomach contents data, which are complex, time-consuming, and expensive to collect (Link 2004, Albouy et al. 2011). The main difficulty in stomach contents analysis is the taxonomic identification of all prey items. Thus, diet composition data are often scarce in the literature, either available for well-known fish species only, or lacking taxonomic details. When no data is available, fish diet composition is either obtained from literature data on similar species, or arbitrarily defined based on expert knowledge. As a consequence, fish diet composition is one of the most poorly estimated parameters in quantitative food web analyses (Link 2004).

In the absence of data, predicting fish diet composition may be challenging, since several factors may influence the diet composition of fish species. Indeed, most fish are generalist feeders, i.e. feed on a broad range of prey items, and also are opportunists when they feed, i.e. they take advantage of available sources of food in their environment (Gerking 1994, Link 2004). Nevertheless, when several prey items are available, fish select certain prey items among all available based on some constraints. Feeding selectivity may be defined as the active or instinctive choice of eating some of all the possible prey items (Link 2004). The challenge is to identify the main constraints that influence fish feeding selectivity.

Size was identified as an important parameter in predator-prey interactions (Cohen et al. 1993, Thiebaux and Dickie 1993, Gill 2003). However, characteristics other than size may influence prey preference and use by fish species (Gerking 1994), such as swimming capabilities (Webb 1984, Palomares and Pauly 1989). Prey preference may be defined as the favored choice of the predator for the most suitable prey items, whereas prey utilization (or diet composition) corresponds to the actual preference, coupled with prey availability (Link 2004). In a few cases, fish diet composition was predicted based on a suite of characteristics describing predator and

prey species (Sibbing and Nagelkerke 2001, Link 2004). However, there is no strong consensus in the literature on good predictors of fish diet composition.

In this study, contrary to most studies in the literature presenting field-based approaches, we used one of the most important open-access, digital and cross-disciplinary data source on fish biodiversity: FishBase (www.fishbase.org). FishBase is a biodiversity information system (BIS), consisting of three components: a database, a website, and analytical tools (Palomares and Bailly 2011). The prototype of FishBase was created in 1988 and the first version of FishBase was released in 1993 (Froese and Pauly 2000). Then, FishBase released CD-ROMs annually from 1994 to 2000 and went online in 1998 (Froese and Pauly 2000). FishBase is an information repository compiling expert-reviewed data describing more than 32,000 fish species of the world, extracted from over 40,000 scientific publications (Froese 2011). The taxonomic authority list and standard nomenclature reference for species scientific names used in FishBase is the "Catalog of Fishes" released by Eschmeyer in 1998 (Palomares and Bailly 2011).

Initially, FishBase was created to fulfill the needs of classical fisheries management, but it has rapidly evolved to include other aspects related to fish biology and ecology, notably with the development of ecosystem-based fisheries management approaches (Palomares and Bailly 2011). Thus, FishBase has progressively become one of the largest databases documenting global fish biodiversity, and is now a well-known and widely-used source of information in the scientific community (Palomares and Bailly 2011). The primary intention of FishBase was to make "a large amount of empirical data [...] available [...] at one's fingertips" (Palomares and Bailly 2011).

In our approach, we intended to identify predictors of fish feeding selectivity by using information readily available in FishBase. More precisely, we intended to test a wide range of parameters (morphological but also anatomical, behavioral or ecological) describing fish species, which have been provided in the literature and encoded in FishBase. First, we selected in FishBase available information on diets and species characteristics of marine and estuarine fish. We focused on trophic interactions between fish species, thus we selected information for piscivorous fish (fish preying on fish) and their corresponding fish prey only. The scope of the study was defined by the availability of the diet data in FishBase, which was mostly representative of the North Sea. We considered a wide range of parameters describing the defined pool of predator and prey fish species. We selected, compiled and formatted the diet data and species parameters and performed statistical analyses so as to: (i) discriminate predator species based on their diets; and (ii) correlate diets to predator and prey species traits described by significant parameters.

5.2. Methods

5.2.1. Definition of the species pool

We started by defining the pool of fish species to be considered for the analyses. In FishBase, we selected marine and/or estuarine species, whose status was native or introduced or endemic, and whose life stage included adults. We restricted our selection to species associated with the North Sea and Baltic Seas ecosystems. Indeed, the International Council for the Exploration of the Sea (ICES) 'Year of the Stomach' dataset was the largest dataset on fish diets recorded in FishBase (version accessed on January 31 2013) and comprises datasets of fish stomach contents for the North Sea (ICES 2010). The data was collected in 1981, 1985-1986, and 1991, then standardized, quality-controlled and made downloadable online in 2010, and it was integrated into the FishBase database in 2012. Besides, the 'Year of the Stomach' dataset has previously been used to develop Ecopath with Ecosim models of the North Sea (Christensen 1995b, Mackinson and Daskalov 2007). The North Sea ecosystems accounted for 73% of all the recorded diet analyses in FishBase, 65% of all the diet records, and 88% of all the recorded diet items identified as fish species in FishBase. In contrast, the Baltic Sea represented about 0.1% of all the recorded diet analyses or records in FishBase. We obtained a pool of 238 fish species, corresponding to 85 families, 36 orders and five classes. In comparison, the total number of species associated with the North and Baltic Seas in FishBase is of 203 and 173, respectively.

5.2.2. Compilation of the diet composition from FishBase

5.2.2.1 Selection of the diet data

In FishBase, we selected the diet data associated with the previously defined pool of 238 fish species. We selected the diets collected in the North and Baltic Seas, and for which the sample size and proportion of empty stomachs were both available, and the sample stage corresponded to adult predator species. We obtained a collection of 44,217 diets (identified by a unique diet code), representing 87% of all the diets stored in the DIET table in FishBase and associated with 163,328 diet items. Then, we screened out the diet items to select only the ones corresponding to adult fish prey species. Of the 163,328 diet items, only 23% corresponded to finfish and only 14% were identified as finfish species. Thus, we obtained a collection of 22,517 diet percents, corresponding to the proportion of each of the adult fish prey identified as species in the diet of the selected adult fish predator species, and representing 11% of all the diet percents stored in the DIET_ITEMS table in FishBase. The selected diet data was referenced from three different sources (Arntz 1978, Malyshev 1980, ICES 2010), though 99.98% of the data came from ICES (2010). Also, the selected diet data was from the Baltic Sea were not associated with an identified fish prey species, and thus were not retained.

5.2.2.2 Calculation of weighted averaged diet percentage for each pair of predator-prey species

The selected diet data was first analyzed in terms of predator and prey species: 31 unique predator species (in 14 families, eight orders and two classes) and 87 unique prey species (in 38 families, 17 orders, and three classes) included in the 22,517 diet percents. Several estimates of diet percents, obtained from different sampling events, were associated with the same pair of predator-prey species. Thus, a weighted averaged diet percentage was calculated for each unique predator-prey pair. Sample sizes were first corrected to take into account the proportion of empty sampled stomachs. Then, the total sample size (accounting for all the different sampling events) was calculated for each predator. The diet percents were weighted by the proportion of total

sample size, and the average value of weighted diet percentage was obtained for each predatorprey pair. The standard error of the mean *SEM* was also calculated, based on the equation:

$$SEM\left(WADP_{ij}\right) = \frac{\sqrt{\frac{1}{(K_j-1)} \times \sum_k (WDP_{ijk} - WADP_{ij})^2}}{\sqrt{K_j}}$$
Equation 5.1

Where $WADP_{ij}$ is the weighted average diet percentage for the predator j – prey i pair; WDP_{ijk} is the weighted diet percentage for the predator j – prey i pair estimated from the sampling event k; and K_j is the total number of sampling events. Based on the 22,517 diet percents from FishBase, we obtained 501 weighted averaged diet percentages and corresponding *SEM*.

5.2.2.3 Conversion of weighted averaged diet percentages into diet composition expressed in percent and rank

Of the 501 calculated weighted average diet percentages, the 132 values obtained for the pairs of selected predator-prey species (see Section 5.2.3) were converted into a diet composition matrix, with the predator species in columns and the prey species in rows. Some predator-prey pairs, with no weighted average diet percentage associated with them, were assumed not to be interacting and attributed zero values. Then, the weighted average diet percentages were summed to one for each predator, so as to obtain a total of 100% for each matrix column. The diet compositions were also expressed in ranks, using ties for equal weighted average diet percentages. Two parameters were then derived from the diet composition matrix: the number of prey for each predator species (*Prey No*), and the predator with the highest proportion of the prey for each prey species (*Predator Max*).

5.2.3. Compilation of the species parameters from FishBase

5.2.3.1 Selection of FishBase fields describing the predator and prey species

Based on a literature review, we selected 159 fields in FishBase corresponding to biological or ecological species parameters. For each field, we first extracted from FishBase the records associated with each of the 31 predator species comprised in the diet data. When more

than one record was associated with the same species in FishBase, the average value was calculated. Records were missing for some species. Thus, among the 31 predator, we selected the species for which more than two thirds of the selected fields were available, and obtained a smaller pool of 14 predator species. Then, among the 159 selected fields, only the ones that were available for all species in the pool were kept. Also, among the available selected fields, some proved to be not discriminative between the 14 predator species and were excluded. Thus, we intended to obtain the optimal selection, comprising the maximum number of fields for the maximum number of species. We obtained a final selection comprising 33 fields describing 14 predator species. We proceeded the same way for prey, and obtained 33 prey species and 30 associated fields. The selection did not comprise exactly the same fields for the predator and the prey species.

The lists of predator and prey species associated with the selection of FishBase fields were compared to the ones associated with the diet percents selection. Only the species listed on both selections were kept. Thus, we ended up with 12 predator species and 31 prey species, associated with 132 weighted averaged diet percentages and described by 31 fields for the predator, and 30 for the prey. Indeed, two fields were not discriminative anymore with the reduced selection of predator species and were excluded.

5.2.3.2 Formatting of the selected predator and prey species parameters

The selected FishBase fields were then formatted so as to perform statistical analyses. Both selections for the prey and the predator species comprised quantitative, qualitative, and Boolean variable types. We chose to convert all fields to qualitative variables. Recorded numbers for quantitative variables were converted to classes, using quartiles for a homogeneous spread of the species in each class. Yes/no records for Boolean variables were also converted to classes, by aggregating some fields so as to have at least one species in each class. After formatting, we ended up with 21 qualitative parameters for the 12 predator species and 18 qualitative parameters for the 31 prey species.

5.2.4. Statistical analyses

We performed multivariate analyses so as to describe and formalize the relationships between the diets, considered as measured variables, and the biological or ecological parameters, considered as explicative variables. We chose to use two exploratory methods, based on linear algebra and using matrix decomposition and orthogonal projection: Principal Component Analysis (PCA) and Correspondence Analysis (CA). The PCA is suitable for quantitative variables, while the CA is the equivalent of a PCA for categorical data and commonly applied to contingency tables. Both analyses were performed using the 'ade4' library of the R software (www.r-project.org/).

First, we performed a centered PCA using the diet composition matrix, with the weighted average diet percentages expressed in rank, the predator species as individuals and the prey species as variables. Moreover, we projected each of the 21 parameters selected for predators, as well as the number of prey, as supplementary variables of the PCA. We intended to identify distinct groups of predators, corresponding to different predator types, and correlated them to biological or ecological traits. Then, we performed a CA using the selected biological and ecological parameters formatted as contingency tables, for the predator and prey species separately. We also used the parameters derived from the diet composition matrix, i.e. the number of prey for each predator (*Prey No*) and the predator with the maximum percentage for each prey (*Predator Max*). Thus, we intended to identify based on species traits, distinct groups of predator and prey, respectively, that we could relate to the diets.

5.3. Results

5.3.1. Pool of predator and prey species

Based on both the diet composition and species parameters compiled from FishBase, we obtained a pool of 12 predator species and 31 prey species (Table 5.1). All species selected as predators are also included as prey, except for one species, the tusk (*Brosme brosme*), so that the selection comprises 32 different species in total. All 32 species belong to the *Actinopterygii*

class. The 12 predator species correspond to members of three different orders: *Perciformes* (one species), *Pleuronectiformes* (one species) and *Gadiformes* (ten species). Among the members of the *Gadiformes*, there are seven species belonging to the *Gadidae* family, two species belonging to the *Lotidae* family, and one species belonging to the *Merlucciidae* family. The prey species comprise members of seven different orders (1 *Anguilliformes*, 1 *Atheriniformes*, 1 *Beloniformes*, 3 *Clupeiformes*, 12 *Gadiformes*, 6 *Perciformes*, and 7 *Pleuronectiformes*) and 16 different families.

5.3.2. Diet composition matrix

Of the 501 weighted average diet percentages and associated standard errors of the mean calculated, only 132 are selected for the analysis (see Appendix D). The diet composition matrix for the pairs of selected predator and prey species is expressed in percentage and in rank (Table 5.2a and Table 5.2b). The number of prey species varies substantially between predator species (Table 5.2a). Two predator species show a large number of prey species: 30 for Atlantic cod (J69) and 24 for whiting (J29). Three predator species show an intermediate number of prey species: 15 for Atlantic mackerel (J118), 14 for haddock (J1381), and 10 for saithe (J1343). The other predator species have a small number of prey species, and tusk (J51) has the lowest number, with only two species. The predator species with the highest proportion of the prey varies between prey species (Table 5.2a). Only one predator does not appear as the species with the maximum value for any prey, saithe (J1343), while whiting (J29) and Atlantic cod (J69) appear the most frequently (for seven prey species each).

5.3.3. Biological and ecological parameters

After the final selection and formatting of the FishBase fields, we obtained 21 parameters for predator and 18 parameters for prey (Table 5.3 and see Appendix E for details). All parameters have been converted to categorical variables, with defined classes or categories, for the purpose of this study. The specific parameters comprise morphological traits of three types: (i) descriptive, including the shape of the body (BS), shape of the caudal fin (CS), attributes of the dorsal fin (DA), shape of the forehead (FS), position of the mouth (MP), attributes of the pelvic fins (PA), specific attributes (such as barbels) (SA), striking features (features may be body shape, fins or mouth) (SF), ventral position (VP and VP2); (ii) morphometric, including the maximum length (ML); and (iii) meristic, including the number of anal fins (AFN), number of barbels (BN), number of dorsal fins (DFN), maximum number of dorsal spines (DSMa), minimum number of dorsal spines (DSMi), and number of keels (KN). The selection also comprises parameters describing the swimming capabilities of the species, including the aspect ratio (AAR, averaged for each species) and swimming Mode (SM), as well as their defensive abilities, with the Dangerous (D) parameter. Several ecological parameters are also selected, describing the preferred type of ecosystem (EsT), environment (ET), and habitat (HT and FWHT) of the species, as well as its maximum depth (DRD). FishBase records corresponding to each selected (and converted when necessary) specific parameter, plus the supplementary parameters derived from the diets (PreyNo and PredatorGroup), are presented separately for the selected predator and prey species (Table 5.4 and Table 5.5). Note that shorthand were used for some of the records, which consisted of long strings of characters, sometimes including symbols, and were shorthanded for programming purposes (original formulations are provided in Table 5.3).

5.3.4. Identification of predator groups

The PCA on the diet composition matrix expressed in rank, with the predator species as individuals, shows that predator groups may be defined based on their diet, and may be related to some specific traits. As observed on the scree plot of Eigen values (Figure 5.1a), the first component contributes to 75% of the total inertia, and the second and third components represent 12% and 8%, respectively. The scattering of the predator species on the factor map of the individuals shows that several groups of predators may be discriminated (Figure 5.1b). When specific parameters are projected as supplementary variables, the distinction between the predator groups appears more clearly. The predator species are spread along the first axis according to their number of prey (PreyNo) (Figure 5.2a and Figure 5.2b). The ordination of the predators on the second axis appears to be related to their maximum length (ML) (Figure 5.3a). The separations between individuals are clearer when they are projected on the plan formed by

the axes 2 and 3 (Figure 5.3b). Along the third axis, individuals seem to be discriminated based on their average aspect ratio (AAR) (Figure 5.4a and Figure 5.4b).

Based on the results from the PCA (Figure 5.2, Figure 5.3 and Figure 5.4), five groups of predators may be defined. Group A consists of whiting (J29) with high number of prey, medium size and medium aspect ratio. Group B corresponds to tusk (J51), which has a very low number of prey. Group C consists of Atlantic cod (J69), with high number of prey, very large size and high aspect ratio. Group D comprises Atlantic mackerel (J118), saithe (J1343), and haddock (J1381), all having a medium number of prey and a very high aspect ratio. The other species compose group E and all have a low number of prey. Thus, the 'Predator Max' parameter, derived from the diet data for each prey species, may be translated into a predator group (PredatorGroup) parameter, by replacing the identified predator species by the predator group to which it belongs (Table 5.5).

5.3.5. Discrimination of prey and predator based on their species traits

The CA on the prey parameters shows that some prey species may be discriminated based on a few parameters. The different levels of each parameter (considered as variables) are projected on the factor map of the individuals (prey species), in the plan formed by the axes 1 and 2 (Figure 5.5). On the upper right side of the plot, a group of prey species may be discriminated based on its number of anal fins (AFN equals two), number of barbels (BN equals one), and number of dorsal fins (DFN equals three). On the lower right side, another group of species may be distinguished according to their minimum number of dorsal spines (DSMi equals six to ten), their environment type (ET is pelagic and neritic), and their freshwater habitat type (FWHT is estuaries and lakes). On the left side, there is one distinct species with a pointed caudal fin, which may be associated with several other species, depending on the parameters considered: (i) either the dorsal fins attributes (DA is continuous with caudal fin), the pelvic fins attributes (PA is suppressed/absent) and the ventral fins position (VP is absent); or (ii) the body shape (BS is eel-like); or (iii) the ecosystem type (EsT is saltwater and brackish water and freshwater). When the 'Predator Group' parameter is projected, there seems to be a dichotomy between prey species whose predator belongs to the groups A and D on the left side, and those whose predator belongs to the groups B, C, and E on the right side, although the distinction is not

clear (Figure 5.6). The CA provides a poor representation of the data, since the first and second axes contribute to only 13% and 12% of the total inertia, respectively.

The CA on the predator parameters does not help to understand the structure of the data. The distribution of the predator species is mainly driven by two species with very distinct traits, while all the other species are aggregated (Figure 5.7). On the upper side of axis 1, one species (Atlantic mackerel, J118) is discriminated from all the other species, based on its dorsal spines maximum and minimum numbers, environment type, keels number, and swimming mode. In contrast, on the right side of the axis 2, another species (megrim, J28) is discriminated due to its body shape, dorsal fin attributes, environment type, striking features, swimming mode, and ventral position. Thus, the swimming mode could explain the spreading of the predator species, with one 'carangiform' species, one 'anguilliform' species and ten other corresponding to 'subcarangiform' species. However, the CA provides a rather poor representation of the data, since the first and second axes contribute to 26% and 21% of the total inertia, respectively.

5.4. Discussion

In this study, we could discriminate several groups of predators (piscivorous fish species) based on the number of prey species they were feeding on, as well as their size and swimming capabilities (defined by the average aspect ratio of their caudal fin). Size and caudal ratio have previously been identified as potential predictors of diet in marine fish assemblages in the literature (e.g., Labropoulou and Markakis 1998, Albouy et al. 2011). However, we could not clearly correlate the predator groups to the biological and ecological traits describing their prey species. Difficulties in the identification of good predictors of fish feeding selectivity may be due to different reasons.

5.4.1. Methodological considerations

First, even if the general approach to analyze fish feeding selectivity is the same between studies, the results may be influenced by the chosen methods and variables of each study (Motta et al. 1995, Norton 1995). For instance, inconsistent results between ecomorphological studies

were assumed to be due to inconsistent methods (Motta et al. 1995). The first issue consists of apriori choosing the appropriate morphological traits (Clifton and Motta 1998), and the second of applying the appropriate statistical analysis. A multitude of multivariate analyses are possible, such as the rather simple PCA and CA performed in this study. More complex methods could have revealed clearer patterns in the data structure in our case. However, in the literature, the most complicated statistical methods that were applied often did not provide conclusive or significant results, apart from the identification of broadly defined trophic guilds (e.g., Boyle and Horn 2006, Albouy et al. 2011).

Ideally, a standard method could be proposed and applied so as to obtain results that would be comparable between studies (Motta et al. 1995). Such method could be based on species traits that would be universally applicable, easily estimated or readily available. In fact, ecomorphological studies for fish commonly focus on one particular taxa or ecosystem, and universality has been very little explored. Thus, in our study, we chose to use FishBase, with the aim of ensuring a wide applicability and eased repeatability of the approach. Originally, we intended to consider as many parameters as possible for as many species as possible. However, data availability was a limiting factor, even for such a large database like FishBase, and we had to use a much reduced selection of species and associated information on diets and traits. Nevertheless, it might actually be better to focus on a few parameters only when analyzing factors of fish feeding selectivity (Norton 1995).

Moreover, the selected data had to be reformatted after extraction from FishBase. Predator diets were averaged by predator species and converted to ranks, while species parameters were converted to qualitative variables using pre-defined classes. The transformation of the data was done so as to make the data readily usable to perform statistical analyses, but could have had an influence on the results of our analyses. For instance, the morphological parameters used in this study consisted mostly of choice fields extracted from FishBase, whereas morphometric data are often used in the literature to describe fish morphology (e.g., Maldonado et al. 2009, Oliveira et al. 2010, Albouy et al. 2011). However, the influence of body size on these morphological measurements must be taken into account when testing them as potential predictors of fish diet (Ibañez et al. 2007).

5.4.2. Potentials and limitations of the use of FishBase

One of the objectives of this study was to use FishBase as a data source to provide new insights on fish feeding selectivity, and it was partially achieved. Using FishBase exclusively, we were able to compile a list of predator and prey species and their associated diets and parameters to be used for performing statistical analyses. The main advantage of using FishBase was that the information was centralized, evaluated, and standardized, notably in terms of species. Thus, the species names associated with both the diet percents and biological or ecological parameters were verified and consistent between the different original sources. Moreover, most information is encoded in FishBase as numeric or choice fields, which facilitates reuse and analyses, contrary to free text (Palomares and Bailly 2011). Lastly, FishBase is structured so as to provide a very detailed description of the recorded diet information, which allowed us to screen out records for which sample size, percentage of empty stomach or prey species names were missing. In that sense, FishBase reached its objective of making empirical data, assembled from already published literature, readily available to facilitate their reuse (Palomares and Bailly 2011).

Nevertheless, some aspects of the reuse of the information extracted from FishBase were more challenging, especially regarding the biological and ecological parameters. Indeed, after the selection of the diet data, we ended up with a pool of 31 predator and 87 prey species. However, after the selection of the parameters, the pool was reduced to 12 predator and 31 prey species. Also, of the 159 FishBase fields of potential interest initially considered for the analysis, only 21 parameters were retained for the predator, and 18 for the prey. Many parameters were missing for many species: only 72% of the parameters were available for the best documented half of the predator species selection based on diets (i.e. 15 predator over 31); and only 64% for the best documented third of the prey species selection based on diets (i.e. 33 prey over 87). Missing parameters in FishBase. Thus, our initial pre-selection of 159 FishBase fields could be an optimistic estimation of the current scientific knowledge. Nevertheless, some fields may also be empty in FishBase because they are not considered as 'active fields' and thus are not filled or updated on a regular basis, such as for some morphological parameters (Froese and Pauly 2000). FishBase fields of potential interest to our approach, which could not be used due to low

availability for the selected species, included the cross section of the body, the caudal attributes, the body weight, morphometric measurements and descriptors of the teeth, gill rakers and scales.

Moreover, some fields were actually available in FishBase, but they could not be reused in our analyses since they were not discriminative, i.e. they had the exact same value for all the selected species. Thus, only 27% of the available fields for the selected predator species, respectively 25% for the prey, happened to be useful to differentiate species. The question of defining parameters to discriminate species is critical when using choice fields, i.e., if choice fields are defined to include every possible case, it may result in slowing down the encoding process (Palomares and Bailly 2011). In FishBase, the minimum number of choices is proposed, including the most frequent cases only (Froese and Pauly 2000). For specific cases, the choice field indicates 'other' and details are provided as free text in related remark fields (Froese and Pauly 2000), but such fields are more difficult to reuse. For instance, the FishBase fields that were not reused in our approach because they were not discriminative included the type of mouth, the type of eyes, or the attributes of the fins.

5.4.3. Challenges in predicting fish feeding selectivity

First, it is important to emphasize that correlation is different from causality (Motta et al. 1995), and approaches such as the one presented here may only describe correlations and assume causality between species traits and diet composition (Norton 1991, 1995). Based on the ecomorphological hypothesis of a correlation between species morphology and ecology, the morphology of the feeding apparatus could be a good predictor of prey utilization for fish (Motta et al. 1995, Norton 1995). However, there is contrasting evidence from the literature to verify the hypothesis of dietary-morphological relationships in fish. Thus, several studies concluded that fish morphology may predict the way fish are feeding (prey preference or feeding mode), but not the prey they feed on (prey utilization or diet composition) (Motta 1988, Motta et al. 1995, Clifton and Motta 1998, Barnett et al. 2006).

Some morphological traits that can be directly related to diet may be good predictors of diet, especially if they are biomechanically relevant (e.g., crushing ability related to hard-shelled prey) (Clifton and Motta 1998). Yet, in many cases, the ecomorphological traits could be used to predict some general aspects of fish feeding only (i.e. trophic guilds, e.g, Boyle and Horn 2006,

Ibañez et al. 2007, Oliveira et al. 2010, Albouy et al. 2011). Possibly, predicting broad trophic guilds of fish species could be relatively easier than, for instance, discriminating piscivorous fish species based on their prey species, as attempted in this study. There may be a greater variability between species belonging to different trophic guilds, rather than between species within the piscivorous trophic guild.

Several factors may influence species morphology, which may as a result be very distantly related to diet (Motta et al. 1995, Norton 1995, Labropoulou and Markakis 1998). Indeed, evolutionary solutions are multiple, and so are the morphological strategies to feeding (Motta 1988). Besides, fish morphology determines swimming capabilities used in foraging activities, but also predation escape (Motta 1988), with a trade-off between prey profitability and predation risk in fish feeding (Labropoulou and Markakis 1998). Thus, in our pool of selected species, all predator species (except for one) were prey items in the diet composition of other predators. Also, both fish morphology and diet may be influenced by habitat utilization (Motta et al. 1995, Barnett et al. 2006). Lastly, the necessity to consider phylogenetic relationships between species in ecomorphological studies is a matter of controversy (Clifton and Motta 1998). Evolutionary history was demonstrated to be more important than ecological history as a factor of influence on fish morphology (Labropoulou and Markakis 1998), especially when many parameters are considered (Norton 1995). It was also argued that species sharing a common ancestor should not be considered statistically independent (Ibañez et al. 2007). Nevertheless, predator-prey interactions may be highly variable between individuals of the same species due to learning capabilities of fish (Kieffer and Colgan 1992, Warburton 2003).

Behavior may be more important than morphology to predict fish feeding selectivity and determine diet composition (Grossman 1986). Despite constraining morphology, fish are able to adapt their diet based on local conditions thanks to their behavioral flexibility (Labropoulou and Markakis 1998, Ibañez et al. 2007). There is a trade-off between morphological and dietary specialization for more efficient feeding, and flexibility allowed by a generalist diet (Norton 1995). Prey utilization is a combination of prey preference and prey availability (Link 2004). Thus, when we predict prey preference based on diet, we ignore the influence of prey availability (Barnett et al. 2006) (likewise, we ignore prey selectivity when we predict diet from prey abundance only). For instance, size is commonly used to predict species interactions in size spectra models (Jennings et al. 2008). Indeed, the relationship between prey size and predator

size has been demonstrated, notably for some fish species in the North Sea (Floeter and Temming 2003, 2005). Our study confirms the potential correlation between the length of the predator fish and their diet composition. However, previous studies also highlighted that the influence of prey availability is stronger than prey size preference on fish diet composition (e.g., North Sea cod; Floeter and Temming 2003).

5.4.4. Recommendations for future studies

Data restriction was the main challenge in our study, as we intended to predict diet composition at the species level, for piscivorous fish species only. The challenges of defining the desirable completeness and level of details in provided information are inherent to any BIS, such as FishBase (Palomares and Bailly 2011). Thus, our approach may highlight some of the strengths and the weaknesses in the current structure and content of FishBase. For instance, some of the fields considered as potentially relevant to our study, but which were not available or discriminative and thus could not be reused, could receive more attention. Overall, we would recommend that future studies relying on FishBase perform an in-depth assessment of the availability and level of details of the FishBase data to be reused, and possibly contribute to the refining of some data if necessary, prior to perform analyses. As FishBase invites, accepts, and acts quickly on critical comments (Palomares and Bailly 2011), we believe that the potentials of the database to be used for future studies are promising.

Code	Predator	Prev	Common Name	Genus	Species	Family	Order	Class
22	no	ricy voc	Patiaulated dragonat	Callionymus	ratioulatus	Callionumidaa	Daraiformas	Actinontorygii
22	110	yes	Drease et		laura		Densiferment	Actinopterygi
23	no	yes	Dragonet	Callionymus	lyra	Califonymidae	Perciformes	Actinopterygii
24	no	yes	Atlantic herring	Clupea	harengus	Clupeidae	Clupeiformes	Actinopterygii
26	no	yes	Witch flounder	Glyptocephalus	cynoglossus	Pleuronectidae	Pleuronectiformes	Actinopterygii
28	yes	yes	Megrim	Lepidorhombus	whiffiagonis	Scophthalmidae	Pleuronectiformes	Actinopterygii
29	yes	yes	Whiting	Merlangius	merlangus	Gadidae	Gadiformes	Actinopterygii
30	yes	yes	European hake	Merluccius	merluccius	Merlucciidae	Gadiformes	Actinopterygii
31	no	yes	Blue whiting	Micromesistius	poutassou	Gadidae	Gadiformes	Actinopterygii
33	yes	yes	Ling	Molva	molva	Lotidae	Gadiformes	Actinopterygii
34	yes	yes	Pollack	Pollachius	pollachius	Gadidae	Gadiformes	Actinopterygii
35	no	yes	European eel	Anguilla	anguilla	Anguillidae	Anguilliformes	Actinopterygii
38	no	yes	Small sandeel	Ammodytes	tobianus	Ammodytidae	Perciformes	Actinopterygii
39	no	yes	Transparent goby	Aphia	minuta	Gobiidae	Perciformes	Actinopterygii
41	no	yes	Mediterranean scaldfish	Arnoglossus	laterna	Bothidae	Pleuronectiformes	Actinopterygii
45	no	yes	Sand smelt	Atherina	presbyter	Atherinidae	Atheriniformes	Actinopterygii
47	no	yes	Garfish	Belone	belone	Belonidae	Beloniformes	Actinopterygii
51	yes	no	Tusk	Brosme	brosme	Lotidae	Gadiformes	Actinopterygii
53	no	yes	Solenette	Buglossidium	luteum	Soleidae	Pleuronectiformes	Actinopterygii
60	no	yes	Crystal goby	Crystallogobius	linearis	Gobiidae	Perciformes	Actinopterygii
66	no	yes	European anchovy	Engraulis	encrasicolus	Engraulidae	Clupeiformes	Actinopterygii
69	yes	yes	Atlantic cod	Gadus	morhua	Gadidae	Gadiformes	Actinopterygii
118	yes	yes	Atlantic mackerel	Scomber	scombrus	Scombridae	Perciformes	Actinopterygii
481	no	yes	Poor cod	Trisopterus	minutus	Gadidae	Gadiformes	Actinopterygii
525	no	yes	Common sole	Solea	solea	Soleidae	Pleuronectiformes	Actinopterygii
1023	yes	yes	Norway pout	Trisopterus	esmarkii	Gadidae	Gadiformes	Actinopterygii
1341	no	yes	European flounder	Platichthys	flesus	Pleuronectidae	Pleuronectiformes	Actinopterygii
1342	no	yes	European plaice	Pleuronectes	platessa	Pleuronectidae	Pleuronectiformes	Actinopterygii

Table 5.1. Nomenclature and taxonomy classification for the 12 predator and 31 prey species selected from FishBase. *Code* corresponds to the code attributed to each species in FishBase.

Code	Predator	Prey	Common Name	Genus	Species	Family	Order	Class
1343	yes	yes	Saithe	Pollachius	virens	Gadidae	Gadiformes	Actinopterygii
1357	no	yes	European sprat	Sprattus	sprattus	Clupeidae	Clupeiformes	Actinopterygii
1367	yes	yes	Pouting	Trisopterus	luscus	Gadidae	Gadiformes	Actinopterygii
1381	yes	yes	Haddock	Melanogrammus	aeglefinus	Gadidae	Gadiformes	Actinopterygii
1876	no	yes	Three-bearded rockling	Gaidropsarus	vulgaris	Lotidae	Gadiformes	Actinopterygii

Table 5.2. Diet composition matrix for selected predator-prey pairs. Species are indicated with their species code in FishBase, with a capital i for prey in rows, and with a capital j for predator in columns. (a) *WADP* values summed to one and expressed in percentage. "_" indicates null values. The last row (*Prey No*) indicates, for each predator species, the number of prey species for which the diet percentages are not null. The last column (*Predator Max*) indicates, for each prey species, the predator species which has the highest the diet percentage. (b) *WADP* values expressed in rank. Ties were attributed the same rank. Null values were ranked last.

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(a)	J28	J29	J30	J33	J34	J51	J69	J118	J1023	J1343	J1367	J1381	Predator Max
122	_	5.9	_	_	_	_	1.1	_	_	_	_	_	J29
I23	11.6	1.3	_	_	_	_	1.2	2.6	_	_	16.2	4.6	J1367
I24	16.6	5.4	15.9	8.1	11.5	50.0	2.6	11.1	14.2	16.4	1.8	10.4	J51
I26	_	0.7	_	_	_	_	1.4	0.1	_	0.3	_	3.2	J1381
128	_	3.7	_	_	_	_	1.1	_	_	_	_	_	J29
129	10.9	4.1	9.2	14.1	9.4	_	2.7	19.7	_	3.2	39.6	5.5	J1367
130	_	2.2	_	_	_	_	_	_	_	_	_	_	J29
I31	_	5.9	_	_	_	_	15.4	6.2	_	6.3	_	_	J69
133	_	_	_	_	_	_	1.5	_	_	_	_	_	J69
I34	_	_	_	_	_	_	12.1	_	_	_	_	2.3	J69
135	_	5.8	_	_	_	_	1.8	_	_	_	_	_	J29
I38	_	4.0	_	_	_	_	9.9	20.5	_	_	_	18.7	J118
I39	_	_	_	_	_	_	0.3	0.1	41.0	_	_	7.6	J1023
I41	_	0.5	_	_	_	_	0.3	0.1	_	_	_	_	J29
I45	_	_	_	_	_	_	6.2	_	-	_	_	_	J69
I47	_	8.7	_	_	_	_	4.4	_	_	_	_	_	J29
153	-	3.1	0.2	_	_	_	0.6	_	_	_	10.7	_	J1367
I60	-	1.4	-	_	_	_	0.4	_	18.1	_	_	_	J1023
I66	-	_	-	_	_	_	0.8	_	_	_	_	_	J69
I69	14.3	2.4	-	21.0	34.0	50.0	2.2	7.4	_	10.8	_	3.4	J51
I118	-	3.3	15.7	19.8	-	_	2.7	1.2	-	19.3	_	_	J33
I481	-	2.6	18.5	_	_	_	1.4	3.2	_	10.7	9.7	_	J30
1525	-	3.1	-	-	-	_	1.0	_	-	_	_	3.2	J1381
I1023	13.4	7.5	15.4	16.0	32.8	_	5.0	11.5	22.8	19.9	_	14.1	J34
I1341	-	14.6	-	-	-	_	2.2	-	-	_	-	-	J29
I1342	-	_	-	_	_	_	0.9	4.3	_	_	_	0.3	J118
I1343	-	1.2	-	-	-	_	12.5	_	-	_	_	4.2	J69
I1357	-	5.3	18.5	_	_	_	1.8	8.2	3.9	3.6	22.0	9.6	J1367
I1367	16.6	3.2	-	-	-	_	1.0	_	-	_	_	_	J28
I1381	16.6	3.9	6.5	21.0	12.2	_	3.6	3.7	_	9.4	_	13.0	J33
I1876							1.8						J69
Prey No	7	24	8	6	5	2	30	15	5	10	6	14	

(h)												
(0)	J28	J29	J30	J33	J34	J51	J69	J118	J1023	J1343	J1367	J1381
I22	6	5	8	6	6	2	22	16	6	11	7	15
I23	4	21	8	6	6	2	20	11	6	11	3	8
I24	1	7	2	5	4	1	11	4	4	3	6	4
I26	6	23	8	6	6	2	18	13	6	10	7	11
I28	6	12	8	6	6	2	21	16	6	11	7	15
I29	5	9	5	4	5	2	9	2	6	9	1	7
I30	6	19	8	6	6	2	31	16	6	11	7	15
I31	6	4	8	6	6	2	1	7	6	7	7	15
I33	6	25	8	6	6	2	17	16	6	11	7	15
I34	6	25	8	6	6	2	3	16	6	11	7	13
I35	6	6	8	6	6	2	14	16	6	11	7	15
I38	6	10	8	6	6	2	4	1	6	11	7	1
I39	6	25	8	6	6	2	29	15	1	11	7	6
I41	6	24	8	6	6	2	30	14	6	11	7	15
I45	6	25	8	6	6	2	5	16	6	11	7	15
I47	6	2	8	6	6	2	7	16	6	11	7	15
153	6	16	7	6	6	2	27	16	6	11	4	15
I60	6	20	8	6	6	2	28	16	3	11	7	15
I66	6	25	8	6	6	2	26	16	6	11	7	15
I69	2	18	8	1	1	1	13	6	6	4	7	10
I118	6	13	3	2	6	2	10	12	6	2	7	15
I481	6	17	1	6	6	2	19	10	6	5	5	15
I525	6	15	8	6	6	2	24	16	6	11	7	12
I1023	3	3	4	3	2	2	6	3	2	1	7	2
I1341	6	1	8	6	6	2	12	16	6	11	7	15
I1342	6	25	8	6	6	2	25	8	6	11	7	14
I1343	6	22	8	6	6	2	2	16	6	11	7	9
I1357	6	8	1	6	6	2	15	5	5	8	2	5
I1367	1	14	8	6	6	2	23	16	6	11	7	15
I1381	1	11	6	1	3	2	8	9	6	6	7	3
I1876	6	25	8	6	6	2	16	16	6	11	7	15

Table 5.3. List of biological and ecological parameters selected for predator and prey species, with associated acronyms and classes or categories. Adapted from FishBase (see Appendix E for details).

Acronym	Parameter	Classes/Categories	Predator	Prey
AAR	Average Aspect Ratio	low (0-0.93); medium (0.94-1.19); high (1.20-1.35); very high (1.36-3.05)	yes	no
AFN	Anal Fins Number	one; two	yes	yes
BN	Barbels Number	zero; one; four	no	yes
BS	Body Shape	eel-like; elongated; fusiform/normal ; short and/or deep	yes	yes
CS	Caudal Fin Shape	forked; truncate; pointed	yes	yes
D	Dangerous	reports of ciguatera poisoning; harmless	no	yes
DA	Dorsal Fin Attributes	continuous with caudal fin; extending over most of the back length; first fin ray very elongated; none; origin on head nearly above eye; other	yes	yes
DFN	Dorsal Fins Number	one; two; three	yes	yes
DRD	Depth Range Deep	shallow (0-274); medium (275-524); deep (525-999); very deep (1000-1075)	yes	no
DSMa	Dorsal Spines Maximum	none (0); one to five $(1-5)$; six to ten $(6-10)$; eleven to fifteen $(11-15)$	yes	yes
DSMi	Dorsal Spines Minimum	none (0); one to five $(1-5)$; six to ten $(6-10)$; eleven to fifteen $(11-15)$	yes	yes
EsT	Ecosystem Type	saltwater; saltwater and brackish water; saltwater and freshwater	yes	yes
ET	Environment Type	bathydemersal; bathypelagic; benthopelagic; demersal; pelagic-neritic; pelagic-oceanic	yes	yes
FS	Forehead Shape	convex; straight	yes	no
FWHT	Freshwater Habitat Type	none; estuaries; estuaries and lakes; estuaries and stream	no	yes
HT	Habitat Type	oceanic; oceanic and neritic; oceanic and neritic and intertidal	yes	yes
KN	Keels Number	zero; two	yes	no
ML	Maximum Length	very small (0-24); small (25-49); medium (50-99); large (100-149); very large (150-200)	yes	yes
MP	Mouth Position	sub-terminal/inferior; superior; terminal	yes	yes
PA	Pelvic Fins Attributes	asymmetric in size/position; normal; other; suppressed/absent	no	yes
SA	Specific Attributes	barbels; none	yes	no
SF	Striking Features	flatfish; fins; mouth; none	yes	yes
SM	Swimming Mode	anguilliform; carangiform; subcarangiform	yes	no
VP	Ventral Fins Position	abdominal; absent; jugular; thoracic	yes	yes
VP2	Ventral Fins Position 2	before origin of D1; behind origin of D1	yes	no

Code	AAR	AFN	BS	CS	DA	DFN	DRD	DSMa	DSMi	EsT	ET
J28	medium	one	shortdeep	truncate	extending	, one	deep	none	none	salt	bathydem
J29	medium	two	fusiform	truncate	none	three	shallow	none	none	salt	benthopel
J30	low	one	elongated	truncate	none	two	verydeep	none	none	salt	dem
J33	low	one	elongated	truncate	none	two	verydeep	none	none	salt	dem
J34	high	two	fusiform	forked	none	three	shallow	none	none	salt	benthopel
J51	high	one	elongated	truncate	continuou	is one	verydeep	o none	none	salt	dem
J69	high	two	fusiform	truncate	none	three	deep	none	none	saltbrack	benthopel
J118	veryhigh	one	fusiform	forked	none	two	verydeep	elevtofift	sixtoten	saltbrack	pelner
J1023	medium	two	fusiform	truncate	none	three	medium	none	none	salt	benthopel
J1343	veryhigh	two	fusiform	forked	none	three	medium	none	none	salt	dem
J1367	low	two	fusiform	truncate	none	three	shallow	none	none	saltbrack	benthopel
J1381	veryhigh	one	fusiform	truncate	none	three	medium	none	none	salt	dem
Code	FS	HT	KN I	ML	MP	SA	SF	SM	VP	VP2	PreyNo
J28	straight	ocener	zero 1	nedium	superior	none	flatfish	anguilliform	jugula	r behind	low

Table 5.4. Parameters selected for the 12 selected predator species. FishBase records are presented using shorthand (see Table 5.3 for the original classes/categories).

Code	FS	HT	KN	ML	MP	SA	SF	SM	VP	VP2	PreyNo
J28	straight	ocener	zero	medium	superior	none	flatfish	anguilliform	jugular	behind	low
J29	straight	ocener	zero	medium	terminal	none	none	subcarangiform	thoracic	before	high
J30	straight	ocener	zero	large	terminal	none	none	subcarangiform	thoracic	before	low
J33	straight	ocener	zero	verylarge	terminal	none	none	subcarangiform	thoracic	before	low
J34	straight	ocener	zero	large	superior	none	none	subcarangiform	thoracic	before	low
J51	straight	oce	zero	large	terminal	barbels	none	subcarangiform	thoracic	before	verylow
J69	straight	ocenerint	zero	verylarge	terminal	barbels	none	subcarangiform	thoracic	before	high
J118	straight	ocener	two	medium	terminal	none	none	carangiform	thoracic	before	medium
J1023	straight	oce	zero	small	superior	barbels	none	subcarangiform	thoracic	before	low
J1343	straight	oce	zero	large	terminal	barbels	none	subcarangiform	thoracic	before	medium
J1367	convex	oce	zero	small	terminal	barbels	none	subcarangiform	thoracic	before	low
J1381	convex	oce	zero	large	inferior	barbels	none	subcarangiform	thoracic	before	medium

Code	AFN	BN	BS	CS	D	DA	DFN
I22	one	zero	fusiform	truncate	harmless	other	two
I23	one	zero	fusiform	truncate	harmless	other	two
I24	one	zero	fusiform	forked	harmless	none	one
I26	one	zero	shortdeep	truncate	harmless	extending	one
I28	one	zero	shortdeep	truncate	harmless	extending	one
129	two	zero	fusiform	truncate	harmless	none	three
I30	one	zero	elongated	truncate	harmless	none	two
I31	two	zero	elongated	truncate	harmless	none	three
I33	one	zero	elongated	truncate	harmless	none	two
I34	two	zero	fusiform	forked	harmless	none	three
I35	one	zero	eellike	pointed	harmless	continuous	one
I38	one	zero	elongated	forked	harmless	continuous	one
I39	one	zero	fusiform	truncate	harmless	none	two
I41	one	zero	shortdeep	truncate	harmless	extending	one
I45	one	zero	elongated	forked	harmless	none	two
I47	one	zero	eellike	truncate	harmless	none	one
153	one	zero	elongated	truncate	harmless	extending	one
I60	one	zero	fusiform	truncate	harmless	other	two
I66	one	zero	elongated	forked	harmless	none	one
I69	two	one	fusiform	truncate	harmless	none	three
I118	one	zero	fusiform	forked	harmless	none	two
I481	two	one	fusiform	truncate	harmless	none	three
1525	one	zero	shortdeep	truncate	harmless	origin	one
I1023	two	one	fusiform	truncate	harmless	none	three
I1341	one	zero	shortdeep	truncate	harmless	origin	one
I1342	one	zero	shortdeep	truncate	harmless	origin	one
I1343	two	one	fusiform	forked	harmless	none	three
I1357	one	zero	fusiform	forked	ciguatera	none	one
I1367	two	one	fusiform	truncate	harmless	none	three
I1381	one	one	fusiform	truncate	harmless	none	three
I1876	one	four	elongated	truncate	harmless	elongated	two

Table 5.5. Parameters selected for the 31 selected prey species. FishBase records are presented using shorthand (see Table 5.3 for the original classes/categories).
Code	DSMa	DSMi	EsT	ET	FWHT	HT
I22	onetofive	onetofive	saltbrack	dem	est	ocenerint
I23	onetofive	onetofive	salt	dem	none	ocener
I24	none	none	saltbrack	benthopel	eststr	ocenerint
I26	none	none	salt	dem	none	oce
I28	none	none	salt	bathydem	none	ocener
I29	none	none	salt	benthopel	none	ocener
I30	none	none	salt	dem	none	ocener
I31	none	none	salt	bathypel	none	ocener
I33	none	none	salt	dem	none	ocener
I34	none	none	salt	benthopel	none	ocener
135	none	none	saltbrackfresh	dem	eststr	oce
I38	none	none	saltbrack	dem	est	ocenerint
139	sixtoten	onetofive	saltbrack	pelner	est	ocener
I41	none	none	salt	dem	none	ocener
I45	sixtoten	sixtoten	saltbrack	pelner	estlak	ocenerint
I47	none	none	saltbrack	peloceanic	none	ocener
I53	none	none	salt	dem	none	oce
I60	onetofive	onetofive	salt	dem	none	ocener
I66	none	none	saltbrack	pelner	estlak	ocener
I69	none	none	saltbrack	benthopel	est	ocenerint
I118	elevtofift	sixtoten	saltbrack	pelner	none	ocener
I481	none	none	salt	benthopel	none	oce
1525	none	none	saltbrack	dem	est	ocenerint
I1023	none	none	salt	benthopel	none	oce
I1341	none	none	saltbrackfresh	dem	eststr	ocenerint
I1342	none	none	saltbrack	dem	est	ocenerint
I1343	none	none	salt	dem	none	oce
I1357	none	none	saltbrack	pelner	est	ocener
I1367	none	none	saltbrack	benthopel	none	oce
I1381	none	none	salt	dem	none	oce
I1876	none	none	salt	dem	none	oce

Code	ML	MP	PA	SF	VP	PredatorGroup
I22	verysmall	terminal	normal	fins	jugular	А
I23	small	terminal	other	fins	jugular	Е
I24	small	superior	normal	none	abdominal	В
I26	medium	superior	normal	flatfish	jugular	D
I28	medium	superior	normal	flatfish	jugular	А
129	medium	terminal	normal	none	thoracic	Е
130	large	terminal	normal	none	thoracic	А
I31	medium	terminal	normal	none	thoracic	С
133	verylarge	terminal	normal	none	thoracic	С
I34	large	superior	normal	none	thoracic	С
135	medium	terminal	absent	fins	absent	А
I38	verysmall	superior	absent	none	absent	D
139	verysmall	terminal	normal	none	thoracic	Е
I41	small	terminal	asymmetric	flatfish	thoracic	А
I45	verysmall	terminal	normal	none	abdominal	С
I47	medium	terminal	normal	mouth	abdominal	А
153	verysmall	inferior	normal	flatfish	jugular	Е
I60	verysmall	superior	normal	mouth	thoracic	Е
I66	verysmall	inferior	normal	none	abdominal	С
I69	verylarge	terminal	normal	none	thoracic	В
I118	medium	terminal	normal	none	thoracic	Е
I481	small	terminal	normal	none	thoracic	Е
1525	medium	inferior	normal	flatfish	jugular	D
I1023	small	superior	normal	none	thoracic	Е
I1341	medium	superior	normal	flatfish	thoracic	А
I1342	large	superior	normal	flatfish	thoracic	D
I1343	large	terminal	normal	none	thoracic	С
I1357	verysmall	terminal	normal	none	abdominal	Е
I1367	small	terminal	normal	none	thoracic	Е
I1381	large	inferior	normal	none	thoracic	Е
I1876	medium	terminal	normal	fins	thoracic	С



Figure 5.1. Results from the PCA on the diet matrix expressed in rank, with the predator species as individuals: (a) scree plot of Eigen values and (b) scatter diagram of the coordinates (or factor map) of the individuals.



Figure 5.2. Results from the PCA: factor map of the individuals with the number of prey (PreyNo) projected as a supplementary variable on the plan formed by (a) axes 1 and 2 and (b) axes 1 and 3.



Figure 5.3. Results from the PCA: factor map of the individuals with the maximum length (ML) projected as a supplementary variable on the plan formed by (a) axes 1 and 2 and (b) axes 2 and 3.



Figure 5.4. Results from the PCA: factor map of the individuals with the average aspect ratio (AAR) projected as a supplementary variable on the plan formed by (a) axes 1 and 3 and (b) axes 2 and 3.



Figure 5.5. Results from the CA on the prey parameters, with the prey species as individuals: factor map of the individuals with the different levels of each parameter projected on the plan formed by the axes 1 and 2. Arrows of different colors indicate species that may be discriminated.



Figure 5.6. Results from the CA on the prey parameters: factor map of the individuals with the group of the predator (PredatorGroup) with the highest diet composition value projected as a supplementary variable on the plan formed by the axes 1 and 2.



Figure 5.7. Results from the CA on the predator parameters, with the predator species as individuals: factor map of the individuals with the different levels of each parameter projected on the plan formed by the axes 1 and 2. Arrows of different colors indicate species that may be discriminated.

6. Conclusion

In this thesis, I performed comprehensive literature reviews and global meta-analyses to build on existing knowledge for providing new insights on trophic interaction between marine species (MSTI). In the Introduction (Chapter 1), I briefly summarized current knowledge on the importance of MSTI and the approaches used to model and predict them. Trophic interactions correspond to feeding relationships between predators and prey, and may have significant effects on marine communities and ecosystems through changes in species abundance (Chapter 1). Anthropogenic drivers, such as fishing activities or human-induced climate change, were identified as important factors of change in MSTI (Chapter 1). The removal of top predators by fishing results in the loss of trophic interactions, and may have consequences for ecosystem functions and services ('trophic downgrading', Estes et al. 2011). Ecosystem-based management approaches were introduced to maintain desirable state and processes at the ecosystem level, and ecosystem models were used as tools for simultaneously considering all components of the ecosystem (Chapter 1). The Ecopath with Ecosim (EwE) trophodynamic model was notably developed to inform ecosystem-based fisheries management (Christensen and Walters 2005, Christensen and Walters 2011).

In the subsequent chapters of my thesis, the analysis of MSTI was structured around three main concepts: feeding selectivity, food web and keystone species. Each concept may be expressed and measured by applying some specific parameters: diet composition (DC), mixed trophic impact (MTI), and index of keystoneness (KS), respectively. These parameters describe the importance of trophic interactions at the species level, and are directly related to one another: the KS index is based on MTI values, which are derived from DC estimates. All parameters were obtained from global information repositories, used as sources of a large amount of digital and standardized data and metadata. DC estimates were calculated from referenced diet records encoded in FishBase, while estimates of MTI and KS index were derived from published EwE models compiled in EcoBase.

Chapter 2 provided an overview of the EwE applications worldwide over the last 30 years, and gathered in the EcoBase repository. Based on the compilation of 433 models associated with 397 publications and 23 sets of metadata, I described how the EwE modeling

approach has been used to study MSTI. Such a comprehensive review has not previously been done in the literature. Overall, the majority of EwE applications corresponded to Ecopath models of (temperate or tropical) marine ecosystems located in the (Northern or Central) Atlantic Ocean, which were developed to analyze ecosystem functioning and fisheries. Through time, the number of published EwE models has been growing, so that all FAO areas comprise at least one model in 2014. Over the last three decades, the complexity and spatial scale of the models have been increasing (larger number of groups and wider range of model area), and more and more Ecopath models were built to represent a given ecosystem at different periods of time. While a significant number of dynamic (Ecosim) versions of the models have been developed, spatially-explicit (Ecospace) versions have remained sparse. The research questions addressed using EwE models and the types of modeled ecosystems have progressively become more diverse (e.g., high latitudes, terrestrial systems). Thus, Chapter 2 demonstrated the growing contribution of the EwE modeling approach to the scientific literature.

The second outcome of Chapter 2 is the standardization and digitization of the metadata describing the EwE models and the corresponding modeled ecosystems. Open-access to these metadata will enable new meta-analyses to be performed, by using them as criteria and applying simple scoring methods to select the models of potential interest (such as what I presented in Chapter 4). Meta-analyses are a growing type of approach in EwE modeling, since they allow getting new insights from current knowledge, by reusing and comparing existing EwE models or EwE-based studies (e.g., Coll et al. 2012, Pikitch et al. 2012, Heymans et al. 2014). In theory, a wide range of metadata could be defined to select published ecosystem models of interest for conducting meta-analyses: general descriptors of the models (such as the ones compiled in Chapter 2), but also input and output parameters (e.g., system indices). However, input and output of EwE models have not yet been made available in EcoBase. The encoding of the data derived from EwE models (with open-access agreement) is the next step in the development of the EcoBase repository (Colléter et al. 2013b).

The description of some metadata (of potentially high relevance) compiled in Chapter 2 was sometimes lacking accuracy or clarity for many models so that the metadata could not be used. Thus, one possible limiting factor to the development of EwE-based meta-analyses could be the varying degree to which models live up to best modeling practices (FAO 2008). Unless standards in modeling practices are defined and enforced, it will remain the modelers'

responsibility to provide detailed information on the objectives, quality and robustness of the models. Nevertheless, the development of EcoBase may encourage modelers to ensure that they give sufficient information to make their models reusable (Colléter et al. 2013b). For instance, in Chapter 2, I identified several metadata that should be systematically provided in the publications presenting the models: location, objectives, area, time period, units, software version, Pedigree index, trophic structure, and environmental conditions. Providing these metadata would facilitate the reuse of EwE models, and thus increase the scientific value of EwE-based publications. Moreover, methodologies allowing diagnostics of EwE models, such as PREBAL (Link 2010), which consists of a set of standard criteria to evaluate network models before the balancing step, could be applied as standard tools when building a model. The Ecopath Research and Development Consortium is working on promoting such best modeling practices within the EwE community (Steenbeek et al. 2014).

Chapter 3 and 4 focused on the concept of keystone species, a metaphorical and ecological term which illustrates the importance of MSTI for ecosystem structure and functioning. In Chapter 3, I analyzed the origin and evolution of the multiple definitions, terms, and examples associated to keystone species in the peer-reviewed literature. I demonstrated the expansion of the concept over time, which had become an over-used concept with a catch-all definition. Originally applied to predator species in aquatic food webs, the concept was later progressively applied to wide variety of species playing various roles in the food web (e.g., keystone prey, keystone competitor, keystone plant), and was subsequently applied at smaller or larger scales and detached from the notion of species (e.g., keystone habitats, keystone communities, keystone individuals) (Chapter 3). Several typologies were proposed in the literature, introducing ambiguity and confusion around the definition of keystone species (e.g., Mills et al. 1993, Bond 1994). In Chapter 3, I argued for a restored definition for keystone species, based on a historical review of the usages and misusages of the term. First, I placed the keystone species concept in a larger conceptual framework, describing different categories of species of potential ecological or managerial interest. Keystone species were notably compared to and differentiated from flagship species, ecosystem engineer species, and foundation species. Then, I proposed an operational definition for keystone species, based on restrictive and specific ecological criteria. I defined a keystone species as a species of high trophic level and low

biomass, which exerts a high and wide impact on the food web, relative to the other species in the community (Chapter 3). The restored definition is consistent with the original concept of 'keystone predator' (Paine 1966, 1969a, Paine 1969b). Moreover, while the keystone species concept has been described as a catch-all and so useless concept (e.g., Cottee-Jones and Whittaker 2012), the restored definition, based on precise and operational criteria, may help prevent from the possible demise of the concept.

Chapter 3 is based on a literature review, which was not exhaustive given that not every single publication mentioning the term 'keystone' was considered, but which was rather focusing on and taking as starting point previous detailed review articles (e.g., Bond 1994, Power et al. 1996, Menge and Freidenburg 2001). I selected the publications that proposed accurate (although sometimes contradictory) definitions and specific examples of the keystone species concept. Also, since the concept has been applied in all types of system (marine, freshwater and terrestrial), the proposed review was not restricted to marine applications. Nonetheless, the overall focus of my thesis being on marine systems, detailed considerations of the concept were slightly more focused on marine species.

Empirical validation of the definition proposed in Chapter 3 may still be debatable, since it is built on a conceptual framework and theoretical considerations (Cottee-Jones and Whittaker 2012). Nonetheless, the restored definition intended to solve the terminological confusion around the keystone species concept and other (more or less) related ecological concepts (Caro 2010). Thus, the proposed conceptual framework may serve to differentiate examples of misusages from appropriate applications of the keystone species terminology in the literature. Among the numerous examples labeled as keystone species in the literature, I selected a few seminal (the most frequently cited) examples of sensu stricto keystone species and pseudo keystone species (Chapter 3). Other case studies, not listed in Chapter 3, may be compared to the definitions established in the suggested framework and identified either as true keystone species or as another species category. Besides, the historical review I conducted in Chapter 3 illustrates the importance of consensus definition and operational criteria for the applicability and usefulness of ecological concepts such as keystone species. Some concepts describing other species categories of potential interest, considered in Chapter 3, were also recently reviewed and refined in the literature: wasp-waist species (Atkinson et al. 2014), ecosystem engineer species (Romero et al. 2014), and umbrella species (Branton and Richardson 2011).

In Chapter 4, I applied the restored definition proposed in Chapter 3 and proposed a new functional index of keystoneness (KS) to identify potential keystone species in marine food webs. The novel KS index is calculated by combining a component estimating trophic impact and a component measuring biomass proportion of the species, both derived from the Ecopath modeling approach (Chapter 4). I selected the proposed index from a suite of 12 alternative KS indices (including two indices directly adapted from the literature). The KS indices were tested by applying them to a collection of 101 published Ecopath models selected from EcoBase, and by confronting two statistical methods (rank correlation tests and a classification tree). I selected the KS_3 index, which obtained positive results with both methods for the majority of the models used in the meta-analysis (Chapter 4). Moreover, I demonstrated that the selected index performed better than existing KS indices in the literature (Power et al. 1996, Libralato et al. 2006) and gave results more consistent with the theoretical definition of keystone species (Chapter 3). Thus, the outcomes of Chapter 4 help improve our understanding of the importance of MSTI, as well as our modeling methods to study them.

Although keystone species is a much debated concept (e.g, Cottee-Jones and Whittaker 2012), it has been widely applied in the literature (e.g., Lewinsohn and Cagnolo 2012), and frequently implemented in recently published EwE applications (e.g., Eddy et al. 2014). The Keystoneness Analysis plug-in, consisting of the two existing KS indices proposed in the literature (Power et al. 1996, Libralato et al. 2006), was used in 11% (47 models) of the models compiled in EcoBase (Chapter 2). Indeed, the concept of keystone species is useful to managers since it potentially allows for the management of a single focal species with the aim of maintaining the whole ecosystem (Perry 2010). The new KS index proposed in Chapter 4 was expressed by following the same approach as in existing indices, so that it could be easily implemented in the EwE plug-in. Thus, the proposed KS index may be reused to inform marine biodiversity conservation, and may also be applied to freshwater and terrestrial systems. Chapter 4 showed that the contributions of the trophic impact and biomass components were better balanced in KS_3 than in the previous indices. Thus, the proposed KS index helps addressing some of the inconsistencies and weaknesses of existing indices that have been observed in the literature (e.g., Coll and Libralato 2012, Valls et al. 2012). In addition, the classification tree proposed in Chapter 4 may also be implemented in EwE and serve as a novel representation of the modeled food web, through a continuum of species defined by their trophic interactions and abundance. Thus, potential keystone species could be quickly identified and compared to other species in the community, as well as abundant or rare species (along the biomass axis) and strong or weak interactors (along the trophic impact axis) in the food web. The benefits of using classification trees in ecological studies, compared to more traditional statistical techniques, notably include the ease of construction, exploration, and interpretation of complex ecological patterns and processes (De'ath and Fabricius 2000). Moreover, classification trees, as well as Spearman rank correlation tests, can deal with non-linear relationships (De'ath and Fabricius 2000).

Chapter 4 constitutes the first meta-analysis of Ecopath models based on metadata from EcoBase reused as selection criteria. Moreover, the application of the selected KS index to a large number of models, representing a wide variety of marine ecosystems, allows drawing some general conclusions. Notably, results from the KS_3 index suggested that toothed whales and sharks are the most common keystone species in marine food webs, which may be confirmed by empirical observations, such as for the Prince William Sound food web (Chapter 4). However, uncertainties in the structure (e.g., the aggregation of the species in functional groups) and outcomes of the Ecopath models may have an influence on the estimation of the KS index (Link et al. 2012). More precisely, the performance of highly aggregated models may be reduced, especially if the species playing critical ecological roles, such as keystone species, are overaggregated (Fulton et al. 2003). Thus, further analyses should focus on the sensitivity of the KS index to the degree of trophic aggregation in the modeled food webs. A minimum number of functional groups as well as a maximum level of aggregation of high trophic level groups might be required for the KS index to be robust. In comparison, structural indices derived from Ecological Network Analyses and used to estimate keystoneness were demonstrated to be robust to uncertainty related to model construction errors (Fedor and Vasas 2009). Model uncertainty may also be analyzed in terms of sensitivity of the KS index to the estimates of biomass and diet composition of the species, since the index is calculated from these two input parameters. Ecopath models were previously demonstrated to be more sensitive to biomass than diet composition (Essington 2007). Besides, semi-quantitative approaches could be used to test the sensitivity of the KS index to MTI values (Rochette et al. 2009).

As briefly reviewed in Chapter 1, human activities represent strong drivers of change in the oceans and have significant and synergistic effects on MSTI. As a consequence, fishing and climate change may impact keystone species (e.g., Harley 2011, Eddy et al. 2014). As discussed in Chapters 3 and 4, context-dependency is one of the major challenges for the identification and management of critical species, such as keystone species. Thus, further analyses could focus on the sensitivity of the KS index to different levels of fishing pressure or changes in environmental conditions. More precisely, uncertainty in the outcomes of the analyses performed in Chapter 4 could be assessed. Using statistical methods, the statuses obtained (including the No Keystone status) and the keystone groups identified for each model could be correlated with the characteristics of the modeled ecosystems. Besides, contrary to previous studies, fishing fleets defined in exploited modeled ecosystems were included (roughly aggregated as one predator group) in the keystoneness analyses presented in Chapter 4. Thus, the category associated to the All Fleet group in the classification tree could potentially be correlated with the type, size, or level of exploitation of the modeled ecosystems. The relevance of integrating economic (e.g., fisheries) and ecological systems has been discussed in the literature (e.g., O'Neill and Kahn 2000).

Chapter 5 presented exploratory analyses of feeding selectivity in predatory fish species, which could allow for more formal predictions of MSTI. My intention with Chapter 5 was to build on existing large datasets, provided in the FishBase biodiversity information system, to identify predictors of diet composition (DC) in piscivorous fish species. Correlations between standardized data from stomach contents analyses and a suite of morphological, behavioral and ecological traits (both extracted from FishBase) were tested using multivariate analyses (Principal Components Analysis and Correspondence Analysis). Size and swimming abilities were identified as influencing factors on fish feeding selectivity in the literature (e.g., Labropoulou and Markakis 1998, Albouy et al. 2011). The outcomes of Chapter 5 confirmed the potential significance of these two parameters for determining prey utilization in predatory fish species. However, no clear or consistent pattern was observed, so that no correlation could be established, between the other species characteristics and DC with the selected datasets.

Diet composition is as a critical parameter when identifying critical species in the food web, such as keystone species, since it is used to define trophic interactions. Yet, as briefly introduced in Chapter 1, there are multiple challenges in estimating accurate diet compositions, notably for fish species. The approach presented in this thesis illustrates the challenges related to diet composition data restrictions. Indeed, I chose to use FishBase as data source, with the aim of maximizing available data while ensuring a wide applicability and eased repeatability of the approach. Yet, despite using a large dataset available through FishBase, the taxonomic aggregation of diet information limited the use of available data (to the North Sea ecosystem in my case). To overcome data limitations, it has recently been proposed that frequency of occurrence (expressed in number) could be preferred to diet composition (expressed in volume or biomass), when detailed information is not required, so as to avoid the inherent problems with the collection and estimation of diet composition (Baker et al. 2014). As an alternative, the continuous integration of a growing number of stomach contents analyses in FishBase could help improving data availability. For instance, recent initiatives, such as the Gulf of Mexico Species Interaction (GoMexSI) database and webpage (Simons et al. 2013) and the Integrated Database and Portal for Fish Stomach Records (Dapstom, Pinnegar 2014), will certainly help making progress in the storage and dissemination of diet composition data, and could eventually be integrated into the global FishBase database. In addition, in terms of potential predictors considered in Chapter 5, the required completeness of the data reduced the dataset to a limited number of well-studied species only. Species traits of potential interest to my approach, which could not be used due to low availability or formatting restrictions in FishBase, included descriptors of fish body shape, eyes, mouth, teeth, gill rakers and scales, fin attributes, and morphometric measurements (Chapter 5). Some more flexible statistical methods could have been applied to allow for less restrictive requirements on these parameters. However, the validation of model predictions could have been challenged by natural variability in fish feeding (Link et al. 2012).

In conclusion, the EwE approach has been widely applied to develop marine ecosystem models worldwide. Each of these models provides insights for a better understanding of MSTI, and EwE-based meta-analysis help improve our understanding even further. However, EwE models are data-driven and require detailed data on diet composition. Thus, data availability may be a critical issue when considering some aspects of trophic interactions, especially for modeling and predictions at the species level. That is why open-access sources and data sharing initiatives

within the scientific community, notably through the use of online digital information repositories, are critical. Standardized and discoverable data and models, collected and stored in open-access repositories, are needed for the development of global meta-analyses in marine ecology.

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Appendices

Appendix A: Detailed list of the 433 unique EwE models documented in EcoBase

Table A1. List of the 433 unique EwE models documented in EcoBase (identified with their model number, first author (in alphabetical order), period and location) and their associated publications (identified with their reference code).

Model	First author	Period	Location	Reference(s)
number				code
318	Abarca-Arenas, L.G.	1980-1989	Gulf of Mexico, Tamiahua	130
518	Ainsworth, C.H.	1985-1985	Newfoundland	303
400	Ainsworth, C.H.	1990-1990	Raja Ampat	300,301
401	Ainsworth, C.H.	2005-2005	Raja Ampat	300,509,301
13	Ainsworth, C.H.	1970-1970	Bay of Biscay	13
14	Ainsworth, C.H.	1998-1998	Bay of Biscay	13
194	Ainsworth, C.H.	1750-1750	British Columbia, Northern	172,159,173
195	Ainsworth, C.H.	1900-1900	British Columbia, Northern	172,173,159
196	Ainsworth, C.H.	1950-1950	British Columbia, Northern	173,159,172
197	Ainsworth, C.H.	2000-2000	British Columbia, Northern	172,173,159
691	Akoglu, E.	1960-1969	Black Sea, inner basin	531
692	Akoglu, E.	1980-1987	Black Sea, inner basin	531
693	Akoglu, E.	1988-1994	Black Sea, inner basin	531
694	Akoglu, E.	1995-2000	Black Sea, inner basin	531
402	Albouy, C.	2000-2001	Corsica, Bonifacio Strait Natural Reserve	304
261	Aliño, P.M.	1990-1990	Santiago Island, Bolinao coral reef	162
698	Althauser, L.L.	1990-2001	Weeks Bay, fall	532
696	Althauser, L.L.	1990-2001	Weeks Bay, spring	532
697	Althauser, L.L.	1990-2001	Weeks Bay, summer	532
695	Althauser, L.L.	1990-2001	Weeks Bay, winter	532
36	Alvarez-Hernández, J.H.	1990-1990	Mexico, Caribbean	33
57	Amorim, P.	1990-1992	Guinea-Bissau, continental shelf	51
523	Angelini, R.	1986-1986	Angola shelf	424
190	Angelini, R.		Sao Paulo State, Broa reservoir	158
298	Angelini, R.	1992-1995	Paraná River Floodplain	140
524	Antony, P.J.	2004-2005	Southeast coast of India, Parangipettai	425
700	Arancibia, H.	2000-2000	Chile, central	535,534
701	Arancibia, H.	2005-2005	Chile, central	534,535
	-			

Model number	First author	Period	Location	Reference(s) code
525	Araújo, J.N.	1970-1970	Western Scotian Shelf + Bay of Fundy, NAFO Division 4X	427,437
526	Araújo, J.N.	1973-1973	English Channel, Western	151,152,428
527	Araújo, J.N.	1995-2000	Bay of Fundy	426
528	Araújo, J.N.	1995-2000	Western Scotian Shelf + Bay of Fundy, NAFO Division 4X	426
529	Araújo, J.N.	1995-2000	Scotian Shelf, Western	426
176	Araújo, J.N.	1993-1995	English Channel, Western	152,428,151
229	Aravindan, C.M.	1980-1980	Lake Veli	143
449	Arbach Leloup, F.	2003-2003	Mont St Michel Bay	355
530	Arias-González, J.E.	1999-1999	Campeche Bank, Alacranes Reef	430
531	Arias-González, J.E.	1998-1998	Sian Ka'an Biosphere Reserve, North, Boca Paila	429
532	Arias-González, J.E.	1998-1998	Mahahual	429
533	Arias-González, J.E.	1998-1998	Sian Ka'an Biosphere Reserve, South, Tampalam	429
222	Arias-González, J.E.	1971-1989	Moorea, Barrier reef of Tiahura	89
103	Arias-González, J.E.	1971-1989	Moorea, Fringing reef of Tiahura	89
239	Arreguín-Sánchez, F.	1978-1979	Gulf of California, Central	30,29
238	Arreguín-Sánchez, F.	1992-1998	Gulf of California, La Paz Bay	161
317	Arreguín-Sánchez, F.	1970-1979	Gulf of Mexico, Southwestern	153
320	Arreguín-Sánchez, F.	1987-1987	Gulf of Mexico, Yucatan	154
534	Aydin, K.Y.	1990-1994	Gulf of Alaska	456,455,431
276	Aydin, K.Y.	1979-1985	Bering Sea, Eastern	150
175	Aydin, K.Y.	1981-1990	Bering Sea, Western	150
711	Bacalso, R.T.M.	2010-2010	Province of Bohol, Danajon Bank	543
535	Bănaru, D.	2000-2009	Gulf of Lions	432
536	Barausse, A.	1996-1998	Adriatic Sea, Northern	433
537	Bayle-Sempere, J.T.	2001-2007	Santa Pola Bay, Fish farm	434
114	Beattie, A.	1970-1970	North Sea	97
63	Blanchard, J.L.	1990-1990	Barents Sea	57
64	Blanchard, J.L.	1995-1995	Barents Sea	57
332	Blanchard, J.L.	1990-1990	Barents Sea	57
333	Blanchard, J.L.	1995-1995	Barents Sea	57
509	Bongu, M.M.	2005-2005	Democratic Republic of the Congo coast	307
92	Bozec, Y.M.	1991-1992	Loyalty Islands, Uvea Atoll	81
151	Bradford-Grieve, J.M.		New Zealand, subantarctic plateau	129
119	Brando, V.E.	1996-1996	Orbetello lagoon	106
657	Brando, V.E.	1995-1995	Orbetello lagoon	106
143	Bredesen, E.L.	1990-2000	Orkneys, Georgia, South	122
58	Browder, J.A.	1980-1989	Gulf of Mexico	52
329	Buchary, E.A.	1990-1999	Bali Strait	10
538	Buchary, E.A.	1974-1979	Java Sea	436

Model	First author	Period	Location	Reference(s)
number				code
227	Buchary, E.A.	1950-1950	Iceland, shelf	59
405	Bulman, C.	1986-1991	Australian Shelf, North West	308
407	Bulman, C.	1992-1996	Tasmanian Seamounts Marine Reserve	309
406	Bulman, C.	1994-1994	East Bass Strait	310
40	Bundy, A.	1980-1985	Nova-Scotia, Eastern	34,35
41	Bundy, A.	1995-2000	Nova-Scotia, Eastern	35,34
655	Bundy, A.	1985-1987	Newfoundland	93,526
106	Bundy, A.	1985-1987	Newfoundland	92,93
129	Bundy, A.	1992-1994	San Miguel Bay	112
708	Byron, C.	2003-2008	Rhode Island, Narragansett Bay	540
712	Byron, C.	2005-2008	Rhode Island, highly flushed temperate lagoons	544
130	Campos, W.L.	1994-1995	San Pedro Bay, Leyte Gulf	113
72	Carrer, S.	1994-1994	Lagoon of Venice	66
120	Carrer, S.	1994-1994	Venice, Pallude della Rosa	107
510	Castro, A.	1999-2006	Sao Tome and Principe	311
539	Chaikina, N.	1980-1980	Sea of Okhotsk	438
246	Chávez, E.A.		Celestun lagoon	26
408	Chen, Z.	1997-1999	China Sea, Beibu Gulf	313
409	Chen, Z.	1997-1999	China Sea, Beibu Gulf	312,439
540	Cheng, J.	2000-2000	China Sea, East	440
410	Cheung, W.W.L.	1970-1970	China Sea, North South	314
411	Cheung, W.W.L.	1990-1990	Falkland Islands (Islas Malvinas)	315
620	Cheung, W.W.L.	2000-2000	China Sea, North South	314
34	Christensen, V.	1950-1950	Chesapeake Bay	479,32
35	Christensen, V.	2002-2002	Chesapeake Bay	32,479
412	Christensen, V.	1963-1963	Gulf of Thailand	56
413	Christensen, V.	1974-1974	North Sea	317
415	Christensen, V.	1993-1995	Viet Nam coast, Southwest	318
251	Christensen, V.	1981-1981	North Sea	98
414	Christensen, V.?	1970-1970	Malaysia Peninsula, Western	318,146
149	Christian, R.R.	1994-1994	Gulf of Mexico, Seagrass in St Marks	127
417	Cisneros-Montemayor, A.M.	1970-1970	Baja California Sur	441,320
421	Coll, M.	1975-1975	Adriatic Sea, Northern and Central	324,453
420	Coll, M.	1978-1980	Mediterranean Sea, Northwestern, Catalan Sea, Southern	323
541	Coll, M.	1978-1978	Catalan Sea, South	442
419	Coll, M.	1990-1990	Adriatic Sea, Northern and Central	322
418	Coll, M.	1994-1994	Mediterranean Sea, Northwestern, Catalan Sea, Southern	321
179	Colléter, M.	2003-2003	Sine Saloum estuary, Bolong de Bamboung	155

Model number	First author	Period	Location	Reference(s) code
180	Colléter, M.	2006-2008	Sine Saloum estuary, Bolong de	155
422	Cornejo-Donoso, J.	1990-1999	Bamboung Antarctic Peninsula, Sub-area CCAMLR 48.1	325
33	Cox, S.P.	1990-1998	Pacific Ocean, central	31
423	Criales-Hernández, M.I.	1995-2000	Colombian coast, North, La Guajira	326,521,443
699	Cruz-Escalona, V.H.	1991-1994	Gulf of Mexico, Laguna Alvarado	533
2	Dalsgaard, J.	1980-1989	Prince William Sound	3
424	Daskalov, G.M.	1960-1960	Black Sea	327
93	De La Cruz-Aguero, G.	1982-1983	Veracruz, Mandinga lagoon	82
542	de Mutsert, K.	1986-1990	Breton Sound Estuary	444,445
248	De Paula E Silva, R.	1972-1985	Maputo Bay	83
236	Degnbol, P.	1979-1981	Lake Malawi	75
255	Delos Reyes, M.R.	1820-1820	Manila, Laguna de Bay	68,67
256	Delos Reyes, M.R.	1920-1920	Manila, Laguna de Bay	67,68
73	Delos Reyes, M.R.	1950-1950	Manila, Laguna de Bay	68,67
258	Delos Reyes, M.R.	1968-1968	Manila, Laguna de Bay	68,67
74	Delos Reyes, M.R.	1980-1980	Manila, Laguna de Bay	67,68
260	Delos Reyes, M.R.	1990-1990	Manila, Laguna de Bay	68,67
455	Díaz-López, B.	2004-2007	Sardinian coast, Northeastern, Aranci Bay	328
543	Díaz-Uribe, J.G.	1980-1980	Gulf of California, Northern and Central	446
425	Díaz-Uribe, J.G.	1990-2001	Gulf of California, La Paz Bay and La Ventana Bay	329
426	Dommasnes, A.	1997-1997	Norwegian and Barents Sea	330
544	Downing, A.S.	1977-1977	Lake Victoria, Mwanza Gulf	447
545	Downing, A.S.	1987-1987	Lake Victoria, Mwanza Gulf	447
546	Downing, A.S.	2005-2005	Lake Victoria, Mwanza Gulf	447
547	Duan, L.J.	1981-1981	Pearl River Estuary	449
548	Duan, L.J.	1997-1999	Pearl River Delta	448
549	Duan, L.J.	1998-1998	Pearl River Estuary	449
163	Duarte, L.O.	1997-1997	Gulf of Salamanca	141,142
427	Erfan, A.		Antarctic Peninsula	331
550	Espinosa-Romero, M.J.		Vancouver Island, West coast	450
428	Essington, T.E.	1990-1998	Pacific Ocean, central	332
429	Falk-Petersen, J.	1993-1996	Troms County, Sørfjord	333
551	Feroz Khan, M.		Hosur Taluk, Kelavarapalli reservoir	451
76	Fetahi, T.	2003-2004	Lake Awassa	452,69
717	Field, J.C.	1960-1969	Californian Current, Northern	334,302
521	Field, J.C.	1990-1999	Californian Current, Northern	334,302
511	Fiogbe, E.D.	2005-2005	Benin EEZ	335
430	Freire, K.M.	1970-1970	East Brazil Large Marine Ecosystem	336
552	Frisk, M.G.	1966-1966	Delaware Bay	454

Model	First author	Period	Location	Reference(s)
number				code
431	Fulton, E.	1994-1995	Port Phillip Bay	520,337
432	Fulton, E.	2007-2007	Ningaloo	177,176
307	Galván-Piña, V.H.	1995-1996	Jalisco and Colima	63
125	Gamito, S.	1996-1997	Ria Formosa reservoir	109
305	Garces, L.R.	1972-1972	Sabah, Western	147
304	Garces, L.R.	1972-1972	Sarawak, Western	147
140	Gasalla, M.A.	1998-1999	Brazil Bight, Southern	121
726	Gascuel, D.	1985-1985	Guinea continental shelf	523
725	Gascuel, D.	2004-2004	Guinea continental shelf	523
436	Godinot, O.	1990-2001	Tropical Pacific Ocean, Western Central	339
553	Goldsworthy, S.D.	1991-1991	Great Australian Bight, Eastern	457
54	Gribble, N.A.	1993-1994	GBR, Northern	49,48
554	Griffiths, S.P.	2004-2007	Eastern Tuna and Billfish Fishery	459,458
437	Guarin, F.Y.		Philippines, North West, Lingayen Gulf	340,376
433	Gucu, A.	1955-1965	Black Sea	341
434	Gucu, A.	1980-1980	Black Sea	341
435	Gucu, A.	1990-1990	Black Sea	341
252	Guénette, S.	1963-1963	Aleutian Islands	5,4
7	Guénette, S.	1997-1997	Azores archipelago	8
439	Guénette, S.	1953-1953	Peruvian coast	343
438	Guénette, S.	1963-1963	Alaska, Southeast	4
55	Guénette, S.	1985-1985	Guinea, large area off	50
56	Guénette, S.	1998-1998	Guinea, large area off	50
689	Guénette, S.	1991-1991	Mauritanian Shelf	529
200	Halfon, E.	1991-1991	Lake Ontario	76
555	Han, JH.	2007-2007	Namyang reservoir	460
441	Haputhantri, S.S.K.	2000-2000	Sri Lanka coast	344
188	Harvey, C.J.	1974-1974	Baltic Sea	11
556	Harvey, C.J.	2000-2000	Puget Sound Central Basin	461
442	Heymans, S.J.J.	1963-1963	Eastern Aleutians and Central Gulf of Alaska	346
443	Heymans, S.J.J.	1974-1974	Scotland, Rockall Trough and its seamounts	465,347
444	Heymans, S.J.J.	1977-1986	Gulf of Maine and Georges Banks	345
201	Heymans, S.J.J.	1450-1450	Newfoundland	95
105	Heymans, S.J.J.	1900-1905	Newfoundland	95
107	Heymans, S.J.J.	1985-1987	Newfoundland	91,94
108	Heymans, S.J.J.	1995-1997	Newfoundland	94,91
263	Heymans, S.J.J.		Benguela, Northern	102
115	Heymans, S.J.J.	1956-1956	Benguela, Northern	101,100
135	Heymans, S.J.J.	1964-1964	Sierra Leone, shelf and slope waters off	119
136	Heymans, S.J.J.	1978-1978	Sierra Leone, shelf and slope waters off	119

Model number	First author	Period	Location	Reference(s) code
137	Heymans, S.J.J.	1990-1990	Sierra Leone, shelf and slope waters off	119
690	Hoover, C.	1970-1979	Beaufort Sea, Mackenzie Shelf area	530
447	Hoover, C.	1978-1978	Antarctic Peninsula	349,463
446	Hoover, C.	1970-1970	Hudson Bay	350,462,351
558	Hossain, M.M.	1992-2004	Lake Toya	464
184	Jarre-Teichmann, A.	1983-1993	Weddel Sea, Eastern	7
311	Jarre-Teichmann, A.	1953-1959	Peru, upwelling ecosystem	108
312	Jarre-Teichmann, A.	1960-1969	Peru, upwelling ecosystem	108
124	Jarre-Teichmann, A.	1973-1979	Peru, upwelling ecosystem	108
559	Jia, P.	1986-1989	Lake Gehu	466
445	Jiang, H.	1997-2000	China Sea, East	348,468
709	Jiang, W.	2000-2003	Tasman and Golden Bays	541
512	Kargbo, V.H.	2006-2007	Sierra Leone	352
513	Kay, D.W.	2007-2007	Liberia shelf	353
134	Kitchell, J.F.	1990-1998	Pacific Ocean, central	118
561	Klaer, N.L.	1915-1915	Australian shelf, Southeast	469
562	Klaer, N.L.	1961-1961	Australian shelf, Southeast	469
233	Kolding, J.	1973-1973	Lake Turkana	138
234	Kolding, J.	1987-1987	Lake Turkana	138
563	Langseth, B.J.	1981-1981	Lake Huron	470
564	Langseth, B.J.	1987-1987	Lake Michigan	470
335	Lassalle, G.	1994-2005	Bay of Biscay	171,170
566	Lee, S.I.	1979-1985	Bering Sea, Eastern	473
448	Lees, K.	1973-1973	Irish Sea	354
450	Lercari, D.	1990-2000	Gulf of California, Northern	356
567	Lercari, D.	1992-2007	Arachania, sandy beach	474
568	Lercari, D.	1992-2007	Barra del Chuy, sandy beach	474
569	Li, L.	2005-2005	Strait of Georgia	476
451	Li, Y.	2000-2000	China Sea, East	357
570	Libralato, S.		Adriatic Sea, Northern and Central	358
571	Libralato, S.		Adriatic Sea, Gulf of Trieste, Miramare Natural Marine Reserve	358
452	Libralato, S.	2000-2003	Adriatic Sea, Gulf of Trieste, Miramare Natural Marine Reserve	180,358
155	Liew, H.C.	1984-1985	Terengganu coast	134
266	Lin, HJ.	1998-2001	Kuosheng Bay	64
453	Lin, HJ.	1999-2001	Taiwan, Southwestern, Tapong Bay	359
71	Lin, HJ.	1997-1997	Lagoon Chiku	65
705	Link, S.	1996-2000	Georges Bank	539,538
704	Link, S.	1996-2000	Gulf of Maine	538,539
707	Link, S.	1996-2000	Mid-Atlantic Bight	538,539
706	Link, S.	1996-2000	Southern New England	538,539

Model number	First author	Period	Location	Reference(s) code
454	Liu, PJ.	2001-2003	Taiwan, South, Kenting National Park, Nanwan Bay	360
572	Liu, OG.	2004-2004	Lake Oiandaohu	477
52	Lobry, J.	1991-1998	Gironde estuary	46,478
456	Lozano-Montes, H.M.	2005-2006	Jurien Bay	178,179
284	Machena, C.	1980-1980	Lake Kariba	72
628	Mackinson, S.	1973-1973	North Sea	362
457	Mackinson, S.	1991-1991	North Sea	362
458	Mackinson, S.	1982-1989	Strait of Georgia	361
293	Mackinson, S.	1881-1890	North Sea	99
169	Man, A.	1991-1991	Malaysia Peninsula, Western	146
268	Manickchand-Heileman, S.	1980-1989	Gulf of Paria	163
240	Manickchand-Heileman, S.	1988-1994	Gulf of Mexico, Sonda de Campeche	120
243	Manickchand-Heileman, S.	1980-1989	Gulf of Mexico, Terminos lagoon	135
328	Martell, S.J.D.	1950-1950	Strait of Georgia	128
172	Martell, S.J.D.	1950-1950	Vancouver Island, Western	527
157	Mathews, C.P.	1966-1972	Thames, Sonning	136
269	McCormick Venier, J.	1980-1989	Looe Key	80,175
24	Melgo, J.L.	1986-1986	Carribean Islands	24
282	Mendoza, J.J.	1980-1989	Venezuela shelf	144
49	Mendy, A.N.	1986-1986	Gambia, continental shelf	44
50	Mendy, A.N.	1992-1992	Gambia, continental shelf	45
51	Mendy, A.N.	1995-1995	Gambia, continental shelf	45
66	Mendy, A.N.	1997-1997	Iceland, marine ecosystem (ICES area Va)	60
67	Mendy, A.N.	1997-1997	Iceland, shelf	61
573	Milessi, A.C.	2003-2006	Laguna de Rocha	480
574	Mohamed, K.S.	1999-2001	Arabian Sea	481,482
575	Mohammed, E.	1980-1989	Lancaster Sound region	483
460	Mohammed, E.	1999-1999	Grenada and the Grenadines	363
459	Mohammed, E.	2001-2005	Lesser Antilles Pelagic Ecosystem	364
242	Morales-Zárate, M.V.		Gulf of California, North, Alto Golfo de California	6
576	Morales-Zárate, M.V.	2006-2008	Baja California, Bahia Tortugas	484
270	Moreau, J.	1970-1979	Lake George	71
309	Moreau, J.	1974-1976	Lake Tanganyika	77
193	Moreau, J.	1980-1983	Lake Tanganyika	77
86	Moreau, J.	1985-1986	Lake Victoria	78
235	Moreau, J.	1971-1972	Lake Victoria	79
322	Moreau, J.	1985-1986	Lake Victoria	79
265	Moreau, J.	1970-1980	Parakrama Samudra reservoir	126
95	Moreno, T.	1993-1994	Canary Islands, Maspalomas lagoon	84
116	Morissette, L.	1985-1987	Gulf of St Lawrence, Northern	103,366,365

Model number	First author	Period	Location	Reference(s) code
118	Morissette, L.	1987-1987	Africa, Northwestern	105
296	Morissette, L.	2000-2004	Scotland, Western	367
578	Moutopoulos, D.K.	1998-2006	Ionian Sea, Greek part	486
12	Mustafa, M.G.	1984-1986	Bay of Bengal	12
579	Nascimento, M.C.	2001-2001	Brazil Bight, Southeastern	487
464	Nauen, C.		Baltic Sea, Schlei Fjord	368,319
30	Neira, S.	1992-1992	Chile, central	28
208	Neira, S.	1998-1998	Chile, central	28
580	Neira, S.	1970-1970	Chile, central	181,488,534
581	Niiranen, S.		Baltic Sea	489
81	Nsiku, E.	1977-1996	Lake Malawi	74
302	Nurhakim, S.	1979-1979	Java, central, North coast	165
582	Nuttall, M.A.	1880-1880	Long Island, Great South Bay	490
583	Nuttall, M.A.	1930-1930	Long Island, Great South Bay	490
584	Nuttall, M.A.	1980-1980	Long Island, Great South Bay	490
585	Nuttall, M.A.	2000-2000	Long Island, Great South Bay	490
514	Ogandagas, C.	2005-2005	Gabon shelf	369
48	Okey, T.A.	2000-2001	Floreana Island	43
99	Okey, T.A.	1995-1998	Atlantic Bight, middle	87
465	Okey, T.A.	1986-1992	Gulf of Carpentaria, Albatross Bay	370
466	Okey, T.A.	1990-1990	Gulf of Carpentaria	371
467	Okey, T.A.	1995-1998	Atlantic Bight, Southern	372
279	Okey, T.A.	1994-1996	Prince William Sound	174,2,1
173	Okey, T.A.	1997-1998	Florida shelf, Western	148,528
273	Olivieri, R.A.	1989-1991	Monterey Bay	88
42	Olson, R.J.	1993-1997	Pacific Ocean, Eastern tropical	36,37,459
324	Opitz, S.	1960-1999	Virgin Islands, British	139
468	Orek, H.	1989-1991	Black Sea	373
586	Ortiz, M.	2004-2007	Mejillones Peninsula, Barren Ground habitat	492
587	Ortiz, M.	2004-2007	Mejillones Peninsula, Lessonia trabeculata habitat	492
588	Ortiz, M.	2004-2007	Mejillones Peninsula, Macrocystis integrifolia habitat	492
590	Ortiz, M.	2005-2007	Antofagasta Bay, La Rinconada Marine Reserve	493
618	Ortiz, M.	2005-2007	Antofagasta Bay, La Rinconada Marine Reserve SS1	494
619	Ortiz, M.	2005-2007	Antofagasta Bay, La Rinconada Marine Reserve SS2	494
591	Ortiz, M.		Tongoy Bay, Southern, Puerto Aldea	495,496
592	Ortiz, M.		Tongoy Bay, Southern, Puerto Aldea, Mud habitat	491,495

Model number	First author	Period	Location	Reference(s) code
593	Ortiz, M.		Tongoy Bay, Southern, Puerto Aldea, Sand habitat	495,496
594	Ortiz, M.		Tongoy Bay, Southern, Puerto Aldea, Sand-gravel habitat	495,496
595	Ortiz, M.		Tongoy Bay, Southern, Puerto Aldea, Seagrass habitat	496,495
515	Osei, S.V.	2005-2005	Ghana shelf	374
96	Ould Taleb Ould Sidi, M.M.	1987-1987	Mauritania EEZ	85
97	Ould Taleb Ould Sidi, M.M.	1998-1998	Mauritania EEZ	85
98	Ould Taleb Ould Sidi, M.M.	1988-1998	Mauritania, Bank Arguin	86
217	Palomares, M.L.D.	1980-1989	Etang de Thau	39
221	Palomares, M.L.D.	1990-1991	Garonne river, Toulouse	160
283	Palomares, M.L.D.	1970-1972	Lake Chad	70
596	Panikkar, P.	1995-1996	Wyra reservoir	497
597	Panikkar, P.	2002-2003	Wyra reservoir	497
598	Patricio, J.	1991-1997	Mondego Estuary, South arm, Eutrophic	498
599	Patricio, J.	1991-1997	Mondego Estuary, South arm, Intermediate area	498
600	Patricio, J.	1991-1997	Mondego Estuary, South arm, Meadows area	498
181	Pauly, D.	1980-1989	Gulf of Alaska, Alaska Gyre	156
469	Pauly, D.	1975-1985	China Sea, South	376
470	Pauly, D.	1983-1994	British Columbia Shelf, Southern	375
224	Pauly, D.	1971-1971	Sakumo lagoon	111
471	Pavés, H.J.	1999-2002	Mejillones Peninsula, Antofagasta	377
168	Pedersen, S.A.	1997-1997	Greenland, Western	145
174	Pedersen, S.A.	1991-1992	Greenland, West shrimp grounds	149
602	Pedersen, T.	1993-1996	Troms County, Sørfjord	500
603	Persad, G.	1999-2001	Discovery Bay	501
604	Phong, L.T.	2002-2004	Mekong Delta	502
472	Pinkerton, M.	2000-2003	Te Tapuwae o Rongokako Marine Reserve	378
473	Pinnegar, J.K.	1998-1998	Bay of Calvi	379
474	Piroddi, C.	1964-1964	Ionian Sea, North Eastern	380
475	Piroddi, C.	2007-2007	Ionian Sea, North Eastern	381
476	Polovina, J.J.	1979-1984	Hawaiian Archipelago, Northwestern, French Frigate Shoals	382
478	Preikshot, D.B.	1950-1950	British Columbia Shelf, Southern	383
479	Preikshot, D.B.	1950-1950	Pacific Ocean, North Eastern	383
477	Preikshot, D.B.	1950-1950	Strait of Georgia	383
480	Pruvost, P.	1987-1988	Kerguelen Islands	384

Model number	First author	Period	Location	Reference(s) code
219	Reyes-Marchant, P.	1990-1992	Lake Aydat, Massif Central	42
131	Rivera-Arriaga, E.	1990-1999	Gulf of Mexico, Terminos lagoon	114
481	Rocha, G.R.	1990-1990	Sao Sebastiao Channel	385
624	Rocha, G.R.	1990-1990	Sao Sebastiao Inner Shelf	385
154	Rosado-Solórzano, R.	1980-1989	Gulf of Mexico, Tampamachoco lagoon	133
482	Rosas-Luis, R.	1980-1980	Gulf of California, Central	386
483	Rosas-Luis, R.	2002-2002	Gulf of California, Central	386
713	Ruesink, J.L.	1988-1989	Shakwak Trench, Kluane Boreal Forest Ecosystem Project	545
714	Ruesink, J.L.	1990-1991	Shakwak Trench, Kluane Boreal Forest Ecosystem Project	545
715	Ruesink, J.L.	1992-1993	Shakwak Trench, Kluane Boreal Forest Ecosystem Project	545
716	Ruesink, J.L.	1994-1995	Shakwak Trench, Kluane Boreal Forest Ecosystem Project	545
605	Ruiz, D.J.	2004-2008	Galapagos Islands, Bolivar Channel	518,503
484	Ruzicka, J.J.	2000-2002	Oregon Coast, inner shelf	387
606	Ruzicka, J.J.	2003-2007	Californian Current, Northern	504
216	Rybarczyk, H.	1998-1998	Bay of Somme	14
132	Rybarczyk, H.	1995-1995	Seine estuary	115
325	Salcido-Guavara, L.A.	1994-1997	Gulf of California, Southern	166
607	Salomon, A.K.		Queen Charlotte Islands, Gwaii Haanas National Marine Conservation Area	505
133	Samb, B.	1990-1990	Sene-gambia, continental shelf	116,117
661	Samb, B.	1964-1981	Sene-gambia, continental shelf	117
22	Sánchez, F.	1994-1994	Cantabrian Sea	23
117	Savenkoff, C.	1994-1996	Gulf of St Lawrence, Northern	104,366
145	Savenkoff, C.	1985-1987	Gulf of St Lawrence, Southern	366,124
146	Savenkoff, C.	1994-1996	Gulf of St Lawrence, Southern	124,366
516	Sedzro, K.M.	2000-2000	Togo shelf	388
485	Shannon, L.	1978-1978	Benguela, Southern	390,522,389
192	Silvestre, G.	1989-1990	Brunei Darussalam	17
43	Stanford, R.	1973-1973	English Channel	38
44	Stanford, R.	1995-1995	English Channel	38
104	Stanford, R.	1985-1986	Morocco, Atlantic coast	90
486	Stobberup, K.A.	1981-1985	Cape Verde Archipelago, Coastal ecosystem	391
487	Tam, J.	1995-1996	Humboldt Current Ecosystem, Northern	392
488	Tam, J.	1997-1998	Humboldt Current Ecosystem, Northern	392
490	Taylor, M.H.	1996-1996	Independence Bay	394
489	Taylor, M.H.	1996-1996	Sechura Bay	393
625	Taylor, M.H.	1998-1998	Independence Bay	394
522	Tecchio, S.	2009-2009	Catalan Sea	395

Model number	First author	Period	Location	Reference(s) code
608	Tomczak, M.T.	1974-1974	Baltic Sea, Baltic Proper	506
626	Tomczak, M.T.	1990-1990	Baltic Sea, Curonian Lagoon	396
491	Tomczak, M.T.	1990-1990	Baltic Sea, Gulf of Riga coast	396
492	Tomczak, M.T.	1990-1990	Baltic Sea, Lithuanian Coast	396
493	Tomczak, M.T.	1990-1990	Baltic Sea, Parnu Bay	396
494	Tomczak, M.T.	1990-1990	Baltic Sea, Puck Bay	396
210	Tong, L.	1982-1983	Bohai Sea	16
609	Traore, A.	1995-1996	Lake Ayamé	507
16	Trites, A.W.	1955-1960	Bering Sea, Eastern	15
183	Trites, A.W.	1979-1985	Bering Sea, Eastern	15
495	Tsagarakis, K.	2003-2006	Aegean Sea, North	397
496	Tsehaye, I.	1998-1998	Eritrea, Red Sea coast	398
186	Tudman, P.D.		GBR, Central	157
610	Ullah, M.H.	2005-2006	Bay of Bengal	508
497	Valls, A.	1998-2008	Port-Cros Archipelago	399
28	Vasconcellos, M.	1950-1950	Atlantic Ocean, central	27
29	Vasconcellos, M.	1998-1999	Atlantic Ocean, central	27
111	Vasconcellos, M.	1950-1950	Atlantic Ocean, central	27
112	Vasconcellos, M.	1997-1998	Atlantic Ocean, central	27
144	Vasconcellos, M.		Brazil, Southern	123
323	Vega-Cendejas, M.E.	1985-1990	Gulf of Mexico, Campeche Bank	18
25	Vega-Cendejas, M.E.	1992-1994	Celestun lagoon	524,25
498	Velasco, G.	2001-2001	Brazilian Shelf, South	402,400,401
60	Vibunpant, S.	1997-1997	Gulf of Thailand	55,54,525
290	Vidal, L.	1989-1995	Bahia La Ascencion	9
631	Vidal, L.	1985-1995	Gulf of Mexico Large Marine Ecosystem	510,499
611	Villanueva, M.C.S.	1980-1981	Ebrie lagoon	514,511
612	Villanueva, M.C.S.	1991-1992	Sine Saloum Estuary	512,511
613	Villanueva, M.C.S.	1997-1998	Bagré reservoir	513
614	Villanueva, M.C.S.	2000-2002	Gambie Estuary	511
615	Villanueva, M.C.S.	2000-2001	Lake Nokoue	511,514
616	Villanueva, M.C.S.	2002-2003	Lake Kivu, Congolese part	515
147	Vivekanandan, E.	1994-1996	India, Southwest coast	125
499	Wabnitz, C.C.	2005-2005	Honolulu, Kaloko-Honokohau	403,516
230	Walline, P.D.	1980-1989	Lake Kinneret	73
153	Walters, C.J.	2004-2004	Gulf of Mexico	131
520	Walters, C.J.	1950-1950	Gulf of Mexico, North	405,404
519	Walters, C.J.	1960-1969	Californian Current, Northern	405
629	Wang, Y.	1981-1981	Pearl River Estuary	517
500	Watermeyer, K.	1600-1600	Benguela, Northern	406
504	Watermeyer, K.	1600-1600	Benguela, Southern	407

Model number	First author	Period	Location	Reference(s) code
501	Watermeyer, K.	1900-1900	Benguela, Northern	406
505	Watermeyer, K.	1900-1900	Benguela, Southern	407
506	Watermeyer, K.	1960-1960	Benguela, Southern	407
502	Watermeyer, K.	1967-1967	Benguela, Northern	406
503	Watermeyer, K.	1990-1990	Benguela, Northern	406
126	Watkinson, S.	1951-1955	British Columbia, Rivers Inlet	110
127	Watkinson, S.	1991-1995	British Columbia, Rivers Inlet	110
703	Watson, R.A.	1993-2007	Tasmania	537
702	Whitehouse, A.G.	1985-1995	Chukchi Sea, Eastern	536
517	Williams, A.B.	2005-2005	Nigeria EEZ	408
113	Wolff, M.	1970-1990	Caete estuary	96
53	Wolff, M.	1993-1994	Gulf Dulce	47
212	Wolff, M.		Gulf of Nicoya	53
158	Wolff, M.	1978-1989	Tongoy Bay	137
710	Xu, S.	2007-2008	Pearl river delta, mangrove-based polyculture	542
617	Xu, S.	2006-2007	Northern Hangzhou Bay, coastal artificial ecosystem	519
46	Zeller, D.	1997-1997	Faroe Islands	41,40,435
291	Zetina-Rejón, M.J.	1988-1994	Gulf of Mexico, Campeche Sound	22,19,20,21
241	Zetina-Rejón, M.J.	1984-1986	Huizache-Caimanero lagoon	58
507	Zhang, Y.	1980-1980	Gulf of Maine	409
508	Zhang, Y.	1990-1990	Gulf of Maine	409

Table A2. List of the references of the 397 publications (ordered by reference code (*ID*)) associated to the 433 unique EwE models documented in EcoBase.

ID	Reference
1	Okey T.A., Pauly D.(1999).Trophic mass-balance model of Alaska's Prince William Sound ecosystem, for the post-spill period 1994-1996. Fisheries Centre Research Reports . 136p.
2	Okey T.A., Pitcher T., Cochrane K.(2002).Simulating extreme fishing polices in Prince William Sound, Alaska: a preliminary evaluation of an ecosystem-based policy analysis tool. pp 94-108 In Pitcher T., Cochrane K.,(eds) The Use of Ecosystem Models to Investigate Multispecies Management Strategies for Capture Fisheries . Fisheries Centre Research Reports 10
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5	Heymans S.J.J., Guenette S., Christensen V.(2005).Ecosystem models of the Western and Central Aleutian Islands in 1963, 1979 and 1991. pp 8-83 In Guenette S., Christensen V.,(eds) Food web models and data for studying fisheries and environmental impacts on Eastern Pacific ecosystems . Fisheries Centre Research Reports 13
6	Morales-Zárate M.V., Arreguin-Sánchez F., López-Martinez J., Lluch-Cota S.E. (2004). Ecosystem trophic structure and energy flux in the Northern Gulf of California, México. Ecological Modelling 174 (4). pp 331-345
7	Jarre-Teichmann A., Brey T., Bathmann U., Dahm C., Dieckmann G., Gorny M., Klages M., Plötz J., Schiel S., Stiller M., Battaglia B., Valencia J., Walton D.W.H.(1997).Trophic flows in the benthic shelf community of the eastern Weddell Sea, Antarctica. pp 118-134 In Battaglia B., Valencia J., Walton D.W.H.,(eds) Antarctic communities species, structure and survival. Cambridge University Press.
8	Guénette S., Morato T., Guénette S., Christensen V., Pauly D.(2001). The Azores Archipelago, 1997. pp 241-270 In Guénette S., Christensen V., Pauly D.,(eds) Fisheries Impacts on North Atlantic Ecosystems: Models and Analyses . Fisheries Centre Research Reports 9
9	Vidal L., Basurto M., Zeller D., Booth S., Mohammed E., Pauly D.(2003). A Preliminary Trophic Model of Bahía de la Ascensión, Quintana Roo, Mexico. pp 255-264 In Zeller D., Booth S., Mohammed E., Pauly D.,(eds) From Mexico to Brazil: Central Atlantic Fisheries Catch Trends and Ecosystem Models . Fisheries Centre Research Reports 11
10	Buchary E.A., Alder J., Nurhakim S., Wagey T., Pitcher T.J., Cochrane K.(2002). The Use of Ecosystem- based Modelling to Investigate Multi-species Management Strategies for Capture Fisheries in the Bali Strait, Indonesia. pp 24-32 In Pitcher T.J., Cochrane K.,(eds) The Use of Ecosystem Models to Investigate Multispecies Management Strategies for Capture Fisheries . Fisheries Centre Research Reports 10
11	Harvey C.J., Cox S.P., Essington T.E., Hansson S., Kitchell J.F. (2003). An ecosystem model of food web and fisheries interactions in the Baltic Sea. ICES Journal of Marine Science: Journal du Conseil 60 (5). pp 939-950
12	Mustafa M.G., Silvestre G., Garces L., Stobutzki I., Ahmed M., Valmonte-Santos R.A., Luna C., Lachica- Aliño L., Munro P., Christensen V., Pauly D.(2003).Trophic Model of the Coastal Ecosystem in the waters of Bangladesh, Bay of Bengal. pp 263-280 In Silvestre G., Garces L., Stobutzki I., Ahmed M., Valmonte- Santos R.A., Luna C., Lachica-Aliño L., Munro P., Christensen V., Pauly D.,(eds) . WorldFish Center Conference Proceedings.
13	Ainsworth C., Feriss B., Leblond E., Guénette S., Guénette S., Christensen V., Pauly D.(2001). The Bay of Biscay, France: 1998 and 1970 models. pp 271-313 In Guénette S., Christensen V., Pauly D.,(eds) Fisheries Impacts on North Atlantic Ecosystems: Models and Analyses . Fisheries Centre Research Report 9
14	Rybarczyk H., Elkaim B., Ochs L., Loquet N.(2003). Analysis of the trophic network of a macrotidal ecosystem: the Bay of Somme (Eastern Channel). Estuarine, Coastal and Shelf Science 58 (3). pp 405-421

ID	Reference
15	Trites A.W., Livingston P.A., Mackinson S., Vasconcellos M.C., Springer A.M., Pauly D.(1999).Ecosystem Change and the Decline of Marine Mammals the Eastern Bering Sea: Testing the Ecosystem Shift and Commercial Whaling Hypotheses. Fisheries Centre Research Reports . 106p.
16	Tong L., Tang Q., Pauly D.(2000). A preliminary approach on mass-balance ecopath model of the Bohai Sea. Chinese Jounal of Applied Ecology 11 (3). pp 435-440
17	Silvestre G., Selvanatham S., Salleh A.H.M., Christensen V., Pauly D.(1993).Preliminary Trophic Model of the Coastal Fisheries Resources of Brunei Darussalam, South China Sea. pp 300-306 In Christensen V., Pauly D.,(eds) . ICLARM Conf. Proc
18	Vega-Cendejas M.E., Arreguin-Sánchez F., Hernández M., Christensen V., Pauly D.(1993).Trophic fluxes on the Campeche Bank, Mexico. pp 206-213 In Christensen V., Pauly D.,(eds) . ICLARM Conf. Proc
19	Zetina-Rejón M.J., Arreguin-Sánchez F., Wakida Kusunoki A.T., Solana-Sansores R., Uribe-Martinez J.(2003).Flujos de energía y estructura trófica de la Sonda de Campeche, Suroeste del Golfo de México. pp 49-57 In Wakida Kusunoki A.T., Solana-Sansores R., Uribe-Martinez J.,(eds) Memorias del III Foro de Camarón del Golfo de México y Mar Caribe. Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación; Instituto Nacional de la Pesca.
20	Arreguin-Sánchez F., Pitcher T.J., Cochrane K.(2002).Impact of Harvesting Strategies on Fisheries and Community Structure on the Continental Shelf of the Campeche Sound, Southern Gulf of Mexico. pp 127- 134 In Pitcher T.J., Cochrane K.,(eds) The Use of Ecosystem Models to Investigate Multispecies Management Strategies for Capture Fisheries . Fisheries Centre Research Reports 10
21	Arregun-Sánchez F., Zetina-Rejón M.J., Manickchand-Heileman S., Ramirez-Rodriguez M., Vidal L.(2004).Simulated response to harvesting strategies in an exploited ecosystem in the southwestern Gulf of Mexico. Ecological Modelling 172 (2-4). pp 421-432
22	Arreguin-Sánchez F., Zetina-Rejón M.J., Ramirez-Rodriguez M.(2008).Exploring ecosystem-based harvesting strategies to recover the collapsed pink shrimp (Farfantepenaeus duorarum) fishery in the southern Gulf of Mexico. Ecological Modelling 214 (2-4). pp 83-94
23	Sánchez F., Olaso I.(2004).Effects of fisheries on the Cantabrian Sea shelf ecosystem. Ecological Modelling 172 (2-4). pp 151-174
24	Melgo J.L., Morisette L., Kaschner K., Gerber L., Morissette L., Melgo J.L., Kaschner K., Gerber L.(2009).Food web model and data for studying the interactions between marine mammals and fisheries in the Caribbean ecosystem. pp 53-120 In Morissette L., Melgo J.L., Kaschner K., Gerber L.,(eds) Modelling the trophic role of marine mammals in tropical areas: data requirements, uncertainty, and validation . Fisheries Centre Research Reports 17
25	Vega-Cendejas M.E., Arreguín-Sánchez F.(2001). Energy fluxes in a mangrove ecosystem from a coastal lagoon in Yucatan Peninsula, Mexico. Ecological Modelling 137 (2-3). pp 119-133
26	Chávez E.A., Garduño M., Arreguín-Sánchez F., Christensen V., Pauly D.(1993).Trophic Dynamic Structure of Celestun lagoon, Southern Gulf of Mexico. pp 186-192 In Christensen V., Pauly D.,(eds) . ICLARM Conf. Proc
27	Vasconcellos M., Watson R., Palomares M.L.D., Pauly D.(2004).Mass-balance models of oceanic systems in the Atlantic. pp 171-214 In Palomares M.L.D., Pauly D.,(eds) West African marine ecosystems: models and fisheries impacts . Fisheries Centre Research Reports 12
28	Neira S., Arancibia H., Cubillos L.(2004).Comparative analysis of trophic structure of commercial fishery species off Central Chile in 1992 and 1998. Ecological Modelling 172 (2). pp 233-248
29	Arreguin-Sánchez F., Arcos E., Chávez E.A.(2002).Flows of biomass and structure in an exploited benthic ecosystem in the Gulf of California, Mexico. Ecological Modelling 156 (2). pp 167-183
30	Arreguín-Sánchez F., Calderón-Aguilera L.E., Pitcher T., Cochrane K.(2002).Evaluating harvesting strategies for fisheries in the Central Gulf of California ecosystem. pp 135-141 In Pitcher T., Cochrane K.,(eds) The Use of Ecosystem Models to Investigate Multispecies Management Strategies for Capture Fisheries . Fisheries Centre Research Reports 10

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31	Cox S.P., Essington T.E., Kitchell J.F., Martell S.J.D., Walters C.J., Boggs C., Kaplan I.(2002).Reconstructing ecosystem dynamics in the central Pacific Ocean, 1952 1998. II. A preliminary assessment of the trophic impacts of fishing and effects on tuna dynamics. Canadian Journal of Fisheries and Aquatic Sciences 59 (11). pp 1736-1747
32	Christensen V., Beattie A., Buchanan C., Hongguang M., Martell S.J.D., Latour R.J., Preikshot D., Sigrist M.B., Uphoff J.H., Walters C.J., Wood R.J., Townsend H.(2009).Fisheries Ecosystem Model of the Chesapeake Bay: Methodology, Parameterization, and Model Exploration. NOAA Technical Memorandum . 146p.
33	Alvarez-Hernández J.H., Zeller D., Booth S., Mohammed E., Pauly D.(2003).Trophic Model of a Fringing Coral Reef in the Southern Mexican Caribbean. pp 227-235 In Zeller D., Booth S., Mohammed E., Pauly D.,(eds) From Mexico to Brazil: Central Atlantic Fisheries Catch Trends and Ecosystem Models . Fisheries Centre Research Reports 11
34	Bundy A.(2004). Mass balance models of the eastern Scotian Shelf before and after the cod collapse and other ecosystem changes. Canadian Technical Report of Fisheries and Aquatic Sciences . xii+193p.
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36	Olson R.J., Watters G.M.(2003). A model of the pelagic ecossystem in the eastern tropical Pacific Ocean. Inter-American Tropical Tuna Commission Bulletin 22 (3). pp 135-248
37	Watters G.M., Olson R.J., Francis R.C., Fiedler P.C., Polovina J.J., Reilly S.B., Aydin K., Boggs C., Essington T., Walters C., Kitchell J.F. (2003). Physical forcing and the dynamics of the pelagic ecosystem in the eastern tropical Pacific: simulations with ENSO-scale and global-warming climate drivers. Canadian Journal of Fisheries and Aquatic Sciences 60 (9). pp 1161-1175
38	Stanford R., Pitcher T.(2004). Ecosystem Simulations of the English Channel: Climate and Trade-Offs. Fisheries Centre Research Reports . 103p.
39	Palomares M.L.D., Reyes-Marchant P., Lair N., Zainure M., Barnabé G., Lasserre G., Christensen V., Pauly D.(1993). A Trophic Model of a Mediterranean Lagoon, Etang de Thau, France. pp 224-229 In Christensen V., Pauly D.,(eds) . ICLARM Conf. Proc
40	Zeller D., Reinert J.(2004).Modelling spatial closures and fishing effort restrictions in the Faroe Islands marine ecosystem. Ecological Modelling 172 (2). pp 403-420
41	Zeller D., Freire K., Zeller D., Watson R., Pauly D.(2001). A North-East Atlantic marine ecosystem model for the Faroe Islands (ICES Area Vb): input data. pp 207-212 In Zeller D., Watson R., Pauly D.,(eds) Fisheries Impacts on North Atlantic Ecosystems: Models and Analyses . Fisheries Centre Research Reports 9
42	Reyes-Marchant P., Jamet J.L., Lair N., Taleb H., Palomares M.L.D., Christensen V., Pauly D.(1993). Preliminary Ecosystem Model of a Eutrophic Lake (Lake Aydat, France). pp 95-102 In Christensen V., Pauly D.,(eds) . ICLARM Conf. Proc
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45	Mendy A.N., Palomares M.L.D., Pauly D.(2004). Addendum: The Gambian continental shelf ecosystem in 1992 and 1995. pp 89-94 In Palomares M.L.D., Pauly D.,(eds) West African marine ecosystems: models and fisheries impacts . Fisheries Centre Research Reports 12
46	Lobry J.(2004). Which reference pattern of functioning for estuarine ecosystems? The case of fish successions in the Gironde estuary

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47	Wolff M., Hartmann H.J., Koch V.(1996). A pilot trophic model for Golfo Dulce, a fjord-like tropical embayment, Costa Rica. Revista de Biologia Tropical 44 (Suppl. 3). pp 215-231
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542	Xu S., Chen Z., Li C., Huang X., Li S.(2011). Assessing the carrying capacity of tilapia in an intertidal mangrove-based polyculture system of Pearl River Delta, China. Ecological Modelling 222 (3). pp 846-856
543	Bacalso R.T.M., Wolff M.(2014). Trophic flow structure of the Danajon ecosystem (Central Philippines) and impacts of illegal and destructive fishing practices. Journal of Marine Systems In Press.
544	Byron C., Link J., Costa-Pierce B., Bengtson D.(2011).Modeling ecological carrying capacity of shellfish aquaculture in highly flushed temperate lagoons. Aquaculture 314 (1-4). pp 87-99
545	Ruesink J.L., Hodges K.E., Krebs C.J.(2002).Mass-Balance Analyses of Boreal Forest Population Cycles:

545 Ruesink J.L., Hodges K.E., Krebs C.J.(2002).Mass-Balance Analyses of Boreal Forest Population Cycles Merging Demographic and Ecosystem Approaches. Ecosystems 5 (2). pp 138-158
Appendix B: Example of the Ecopath model of the Prince William Sound (1994-1996)

The Ecopath model representing the Prince William Sound between 1994 and 1996 comprises 48 living groups, plus three dead groups, as well as three fleets representing commercial, recreational and subsidence fisheries (Okey and Pauly 1999). Two graphical representations of the Prince William Sound (1994-1996) food web are given: the flow diagram, representing the biomass and trophic flows of the functional groups (Figure B1), and the MTI plot, representing the relative mixed trophic impact of the functional groups and fishing fleets (Figure B2).



Figure B1. Flow diagram of the Prince William Sound (1994-1996) food web (Okey and Pauly 1999). Each functional group is represented with a gray node, whose size is proportional to the biomass of the group. Trophic flows between groups are represented with lines, with a color scale ranging from 0 to 1. Flows enter a node on its lower part, and exit it from the upper part. The names of the functional groups are indicated next to each node. Functional groups are distributed on the y-axis according to their estimated trophic level.



Figure B2. Mixed Trophic Impact plot of the Prince William Sound (1994-1996) food web (Okey and Pauly 1999). Each functional group is represented as an impacted group in columns, and as an impacting group in rows. A white circle indicates a positive mixed trophic impact of the impacting group on the impacted one, while a black circle indicates a negative mixed trophic impact. The size of the circles is proportional to the importance of the relative impact, ranging from 0 to 1. Fishing fleets are represented in the same way as functional groups.

Appendix C: Overview of the 101 selected Ecopath models

Table C1. Criteria used for the scoring method and final score of the 101 selected Ecopath models, with: model number in EcoBase (*No*); analysis of keystone species previously performed with this model (*KS*); model representing a Marine Protected Area (*MPA*); 'sibling' model(s) available (*Sibling*); model focusing on a (group of) species of particular interest (*Interest*); detailed information on species aggregation into groups available (*Details*); 'overlapping' model(s) available (*Overlap.*); final score of the model (*Score*). Note: the final score was obtained by summing the six criteria scores (1 for "yes" and 0 for "no"), with a coefficient of 2 applied to the first three.

No	KS	MPA	Sibling	Interest	Details	Overlap.	Score
13	1	0	1	0	1	0	5
14	1	0	1	0	1	0	5
28	0	0	1	0	1	0	3
29	0	0	1	0	1	0	3
34	0	0	1	1	1	0	4
35	0	0	1	1	1	0	4
40	1	0	1	1	1	0	6
41	0	0	1	1	1	0	4
48	1	0	0	1	0	0	3
49	0	0	1	0	0	0	2
50	0	0	1	0	0	0	2
51	0	0	1	0	0	0	2
55	0	0	1	0	1	0	3
56	0	0	1	0	1	0	3
66	0	0	1	0	1	0	3
96	0	0	1	0	1	0	3
97	0	0	1	0	1	0	3
98	0	1	0	0	1	0	3
107	1	0	1	0	0	0	4
108	0	0	1	0	0	0	2
115	0	0	1	0	1	0	3
124	1	0	1	1	0	0	5
135	0	0	1	0	1	0	3
136	0	0	1	0	1	0	3
137	0	0	1	0	1	0	3
145	0	0	1	1	1	0	4
182	1	0	1	1	1	0	6
194	0	0	1	0	1	0	3
195	0	0	1	0	1	0	3
196	0	0	1	0	1	0	5
197	0	0	1	0	1	0	5
	-			•			•

No	KS	MPA	Sibling	Interest	Details	Overlap.	Score
202	1	0	1	0	1	0	5
205	1	0	1	1	1	0	6
207	0	0	1	1	1	0	4
208	0	0	1	1	1	0	4
227	0	0	1	0	0	0	2
239	0	0	1	1	1	0	4
251	0	0	1	0	1	0	3
252	0	0	0	1	1	1	3
254	1	0	0	1	0	0	3
271	0	0	1	0	1	0	3
272	0	0	1	0	1	0	3
276	1	0	1	1	1	0	6
277	1	0	0	1	1	0	4
293	1	0	1	0	1	0	5
294	0	0	1	1	1	0	4
295	0	0	1	1	1	0	4
297	0	0	1	0	1	0	3
311	1	0	1	1	0	0	5
312	1	0	1	1	0	0	5
324	0	1	0	0	1	0	3
328	0	0	1	0	0	0	2
400	0	0	1	0	1	0	3
401	0	1	1	1	1	0	6
402	0	1	0	1	1	0	4
407	0	1	0	0	1	0	3
410	0	0	1	0	1	0	3
412	0	0	1	0	1	0	3
413	1	0	1	1	0	0	5
418	0	0	1	0	1	0	3
419	1	0	1	0	1	0	5
420	0	0	1	0	0	0	2
421	0	0	1	0	0	0	2
427	0	0	1	1	1	0	4
429	0	0	1	1	1	0	4
433	0	0	1	1	1	0	4
434	0	0	1	1	1	0	4
435	0	0	1	1	1	0	4
442	0	0	0	1	1	1	3
444	1	0	1	0	1	0	5
450	0	1	0	1	1	0	4
451	1	0	0	0	1	0	3
452	1	1	0	0	0	0	4

No	KS	MPA	Sibling	Interest	Details	Overlap.	Score
454	0	1	0	1	0	0	3
457	0	0	1	0	1	0	3
458	0	0	1	0	1	0	3
462	0	0	1	1	1	0	4
472	0	1	0	0	1	0	3
474	0	0	1	0	1	0	3
475	0	0	1	1	NA	0	3
482	0	0	1	1	0	0	3
483	0	0	1	1	0	0	3
485	0	0	1	0	1	0	3
487	0	0	1	0	1	0	3
488	0	0	1	0	1	0	3
490	0	0	1	1	1	0	4
491	0	1	0	0	1	0	3
494	0	1	0	0	1	0	3
495	1	0	0	0	NA	0	2
497	1	1	0	0	1	0	5
499	0	1	0	1	1	0	4
500	0	0	1	0	1	0	3
501	0	0	1	0	1	0	3
502	0	0	1	0	1	0	3
503	0	0	1	0	1	0	3
504	0	0	1	0	1	0	3
505	0	0	1	0	1	0	3
506	0	0	1	0	1	0	3
507	0	0	1	1	0	0	3
508	0	0	1	1	0	0	3
522	1	0	0	0	1	0	3

Table C2. Metadata of the 101 selected Ecopath models, with: model number in EcoBase (*No*); first author (*Author*); location of the modeled ecosystem (*Location*); type of the modeled ecosystem: bay / fjord, channel / strait, coastal lagoon, continental shelf, coral reef, ocean, or upwelling (*Type*); climatic zone of the modeled ecosystem: temperate, tropical, or polar (*Zone*); first year of the time period represented by the model (*Start*); last year of the time period represented by the model (*Start*); spatial extent covered by the model in km² (*Area*); number of living groups in the model (*Groups*); total biomass of living groups in t·km² (*B_{tot}*); number of groups whose biomass was estimated by Ecopath (*B_{estim}*); model fitted to time-series in Ecosim (*TS*); number of fishing fleets in the model (*Fleets*); total catch of fishing fleets in t·km² (*Y_{tot}*); mean trophic level of the catch (*TL_Y*). Note: "_" indicates no catch.

No	Author	Location	Туре	Zone	Start	End	Area	Groups	Btot	Bestim	TS	Fleets	Ytot	TLY
13	Ainsworth, C.H.	Bay of Biscay	continental shelf	temperate	1970	1970	96,587	36	257	0	yes	5	1.721	3.29
14	Ainsworth, C.H.	Bay of Biscay	continental shelf	temperate	1998	1998	96,587	36	254	11	yes	5	1.191	3.44
28	Vasconcellos, M.	Atlantic Ocean, Central	ocean	tropical	1950	1950	18,419,191	37	159	13	no	1	0.001	4.02
29	Vasconcellos, M.	Atlantic Ocean, Central	ocean	tropical	1998	1999	18,419,191	37	158	12	no	1	0.010	4.26
34	Christensen, V.	Chesapeake Bay	bay / fjord	temperate	1950	1950	18,580	45	242	15	yes	6	24.880	2.46
35	Christensen, V.	Chesapeake Bay	bay / fjord	temperate	2002	2002	18,580	44	116	0	yes	7	12.069	2.42
40	Bundy, A.	Nova-Scotia, Eastern	continental shelf	temperate	1980	1985	100,000	38	245	12	no	12	1.725	3.54
41	Bundy, A.	Nova-Scotia, Eastern	continental shelf	temperate	1995	2000	100,000	38	310	5	no	1	0.490	3.26
48	Okey, T.A.	Floreana Island	coral reef	tropical	2000	2001	6.44	42	2620	10	yes	1	3.125	2.34
49	Mendy, A.N.	Gambia Shelf	continental shelf	tropical	1986	1986	4,000	21	146	7	no	3	5.002	2.96
50	Mendy, A.N.	Gambia Shelf	continental shelf	tropical	1992	1992	4,000	21	160	10	no	1	2.071	3.17
51	Mendy, A.N.	Gambia Shelf	continental shelf	tropical	1995	1995	4,000	21	149	12	no	2	3.175	3.13
55	Guénette, S.	Guinea	ocean	tropical	1985	1985	112,000	34	229	15	no	2	0.909	3.31
56	Guénette, S.	Guinea	ocean	tropical	1998	1998	112,000	43	139	22	no	2	0.868	3.25
66	Mendy, A.N.	Iceland	ocean	polar	1997	1997	376,766	23	3776	10	no	14	5.881	2.85

No	Author	Location	Туре	Zone	Start	End	Area	Groups	Btot	Bestim	TS	Fleets	Ytot	TLY
96	Ould Taleb Ould Sidi, M.M.	Mauritania	ocean	tropical	1987	1987	230,000	37	194	6	no	1	3.325	3.31
97	Ould Taleb Ould Sidi, M M	Mauritania	ocean	tropical	1998	1998	230,000	37	193	5	no	1	4.019	3.05
98	Ould Taleb Ould Sidi, M.M.	Bank Arguin	coastal lagoon	tropical	1988	1998	10,000	21	871	6	no	1	0.391	3.25
107	Heymans, J.J.	Newfoundland	ocean	temperate	1985	1987	495,000	49	311	21	yes	11	1.307	3.85
108	Heymans, J.J.	Newfoundland	ocean	temperate	1995	1997	495,000	49	286	12	yes	11	0.280	3.17
115	Heymans, J.J.	Benguela, Northern	upwelling	tropical	1956	1956	179,000	31	589	10	yes	10	2.291	2.58
124	Jarre- Teichmann, A.	Peru	upwelling	tropical	1973	1979	82,000	19	404	0	no	1	32.177	2.61
135	Heymans, J.J.	Sierra Leone	continental shelf	tropical	1964	1964	27,500	43	61	26	no	2	0.173	2.92
136	Heymans, J.J.	Sierra Leone	continental shelf	tropical	1978	1978	27,500	43	58	31	no	2	0.723	3.12
137	Heymans, J.J.	Sierra Leone	continental shelf	tropical	1990	1990	27,500	43	51	30	no	2	0.771	3.06
145	Savenkoff, C.	Gulf of St Lawrence, Southern (NAFO div. 4T)	continental shelf	temperate	1985	1987	64,075	29	283	6	no	1	57.353	1.11
182	Trites, A.W.	Bering Sea, Eastern	ocean	temperate	1955	1960	484,508	24	303	2	yes	7	2.545	3.42
194	Ainsworth, C.H.	British Columbia, Northern	chanel / strait	temperate	1750	1750	70,000	51	264	0	no	5	0.158	2.86
195	Ainsworth, C.H.	British Columbia, Northern	chanel / strait	temperate	1900	1900	70,000	51	180	0	no	8	0.273	2.34
196	Ainsworth, C.H.	British Columbia, Northern	chanel / strait	temperate	1950	1950	70,000	51	125	1	yes	19	2.128	3.30

No	Author	Location	Туре	Zone	Start	End	Area	Groups	Btot	Bestim	TS	Fleets	Ytot	TLY
197	Ainsworth, C.H.	British Columbia, Northern	chanel / strait	temperate	2000	2000	70,000	51	128	0	yes	17	1.324	3.32
202	Pitcher, T.J.	Newfoundland	ocean	temperate	1900	1905	495,000	49	693	34	no	5	0.878	3.92
205	Morissette, L.	Gulf of St Lawrence, Northern (NAFO div. 4R,S)	chanel / strait	temperate	1985	1987	103,812	31	287	1	no	1	1.490	3.69
207	Neira, S.	Chile, Central	upwelling	temperate	1992	1992	50,042	20	248	5	no	0	_	_
208	Neira, S.	Chile, Central	upwelling	temperate	1998	1998	50,042	20	399	0	no	1	19.420	2.42
227	Buchary, E.A.	Iceland	ocean	polar	1950	1950	376,766	23	3818	22	yes	14	1.975	3.36
239	Arreguín- Sánchez, F.	Gulf of California, Central	chanel / strait	tropical	1978	1979	27,900	25	69	17	yes	4	17.706	2.99
251	Christensen, V.	North Sea (ICES div. IVa,b,c)	continental shelf	temperate	1981	1981	570,000	28	234	9	no	1	4.482	4.08
252	Guénette, S.	Aleutian Islands, W Central	continental shelf	temperate	1963	1963	56,936	39	210	22	yes	6	0.462	3.48
254	Kitchell, J.F.	Pacific, Central	ocean	temperate	1990	1998	30,000	21	9	0	yes	0	_	_
271	Stanford, R.	English Channel	continental shelf	temperate	1973	1973	89,607	43	270	6	yes	0	_	_
272	Stanford, R.	English Channel	continental shelf	temperate	1995	1995	89,607	48	431	6	yes	9	3.102	2.53
276	Aydin, K.Y.	Bering Sea, Eastern	continental shelf	temperate	1979	1985	484,500	35	265	4	no	1	2.989	3.38
277	Aydin, K.Y.	Bering Sea, Western	continental shelf	polar	1981	1990	254,200	33	569	2	no	1	1.659	3.57
293	Mackinson, S.	North Sea (ICES div. IVa,b,c)	continental shelf	temperate	1881	1890	570,000	44	285	11	no	5	0.795	3.77
294	Blanchard, J.L.	Barents Sea	continental shelf	polar	1990	1990	1,400,000	38	119	18	yes	6	0.109	3.98
295	Blanchard, J.L.	Barents Sea	continental shelf	polar	1995	1995	1,400,000	38	119	19	yes	6	218.681	4.11

No	Author	Location	Туре	Zone	Start	End	Area	Groups	Btot	Bestim	TS	Fleets	Ytot	TLY
297	Araújo, J.N.	English Channel, Western (ICES div. VIIe)	chanel / strait	temperate	1993	1995	56,452	50	196	6	yes	9	3.382	2.44
311	Jarre- Teichmann, A.	Peru	upwelling	tropical	1953	1959	NA	19	295	2	no	1	6.491	2.35
312	Jarre- Teichmann, A.	Peru	upwelling	tropical	1960	1969	NA	19	319	2	no	1	91.669	2.22
324	Opitz, S.	British Virgin Islands	coral reef	tropical	1960	1999	NA	20	3902	0	no	0	_	_
328	Martell, S.J.D.	Strait of Georgia	chanel /	temperate	1950	1950	7,000	26	828	5	yes	1	7.950	3.25
400	Ainsworth, C.H.	Raja Ampat	coral reef	tropical	1990	1990	45,000	96	213	4	yes	17	3.034	3.17
401	Ainsworth, C.H.	Raja Ampat	coral reef	tropical	2005	2005	45,000	96	208	6	yes	17	6.850	3.05
402	Albouy, C.	Bonifacio Strait Natural Reserve, S Corsica	continental shelf	temperate	2000	2001	800	31	920	9	yes	3	0.194	3.87
407	Bulman, C.	Tasmanian Seamounts Marine Reserve, SW Tasmania	ocean	temperate	1992	1996	370	24	292	0	yes	0	_	_
410	Cheung, W.W.L.	South China Sea, Northern	continental shelf	tropical	1970	1970	NA	37	544	11	yes	1	0.854	3.19
412	Christensen, V.	Gulf of Thailand	continental shelf	tropical	1963	1963	NA	28	89	10	yes	2	11.664	3.01
413	Christensen, V.	North Sea (ICES div. IVa,b,c)	continental shelf	temperate	1974	1974	570,000	31	276	5	yes	4	6.133	3.89
418	Coll, M.	Catalan Sea, Southern	ocean	temperate	1994	1994	4,500	37	59	0	yes	4	5.356	3.12

No	Author	Location	Туре	Zone	Start	End	Area	Groups	Btot	Bestim	TS	Fleets	Ytot	TLY
419	Coll, M.	Adriatic Sea, Northern Central	continental shelf	temperate	1990	1990	55,500	37	130	4	yes	5	2.445	3.07
420	Coll, M.	Catalan Sea, Southern	ocean	temperate	1978	1980	4,500	37	46	21	yes	4	3.970	3.07
421	Coll, M.	Adriatic Sea, Northern Central	continental shelf	temperate	1975	1975	55,500	37	134	6	yes	5	3.169	3.28
427	Erfan, A.	Antarctic Peninsula	ocean	polar	1990	1991	433,620	38	156	0	yes	1	10.000	2.17
429	Falk-Petersen, J.	Sorfjord and Ullsfjord, N Norway	bay / fjord	polar	1993	1996	55	24	234	0	yes	1	0.531	3.29
433	Gucu, A.	Black Sea	continental shelf	temperate	1955	1965	NA	6	47	2	no	1	0.434	3.22
434	Gucu, A.	Black Sea	continental shelf	temperate	1980	1980	NA	6	1942	3	no	1	1.728	3.06
435	Gucu, A.	Black Sea	continental shelf	temperate	1990	1990	NA	6	701	3	no	1	0.415	3.24
442	Heymans, J.J.	Aleutian Islands, W Central	ocean	temperate	1963	1963	291,840	39	150	20	yes	6	0.369	3.39
444	Heymans, J.J.	Gulf of Maine	continental shelf	temperate	1977	1986	103,000	28	350	7	no	11	1.718	3.53
450	Lercari, D.	Gulf of California, Northern	continental shelf	temperate	1990	2000	36,000	33	178	0	yes	0	-	-
451	Li, Y.	East China Sea	continental shelf	tropical	2000	2000	500,500	37	62	9	no	1	5.905	3.01
452	Libralato, S.	Miramare Natural Marine Reserve, N Adriatic Sea	bay / fjord	temperate	2000	2003	120	18	310	0	yes	0	_	_
454	Liu, PJ.	Nanwan Bay, Kenting National Park, S Taiwan	coral reef	tropical	2001	2003	NA	17	2030	0	no	1	7.280	2.42

No	Author	Location	Туре	Zone	Start	End	Area	Groups	Btot	Bestim	TS	Fleets	Ytot	TLY
457	Mackinson, S.	North Sea (ICES div. IVa,b,c)	continental shelf	temperate	1991	1991	570,000	65	552	9	yes	12	5.668	3.67
458	Mackinson, S.	Strait of Georgia	chanel / strait	temperate	1982	1989	6,900	14	919	0	no	0	_	_
462	Morissette, L.	Gulf of St Lawrence, Northern (NAFO div. 4R,S)	chanel / strait	temperate	1994	1996	103,812	31	280	0	no	1	56.262	1.02
472	Pinkerton, M.	Te Tapuwae o Rongokako Marine Reserve, New Zealand	coral reef	temperate	2000	2003	24.52	21	152	0	no	0	_	-
474	Piroddi, C.	Ionian Sea, North Eastern	continental shelf	temperate	1964	1964	1,021	20	44	0	yes	5	1.087	3.12
475	Piroddi, C.	Ionian Sea, North Eastern	continental shelf	temperate	2007	2007	1,021	17	42	0	yes	5	1.890	3.15
482	Rosas-Luis, R.	Gulf of California, Central	continental shelf	tropical	1980	1980	NA	17	37	0	no	1	1.000	2.84
483	Rosas-Luis, R.	Gulf of California, Central	continental shelf	tropical	2002	2002	NA	17	39	0	no	1	1.080	3.22
485	Shannon, L.	Benguela, Southern	upwelling	temperate	1978	1978	220,000	31	204	12	yes	13	2.798	3.74
487	Tam, J.	Northern Humboldt Current	upwelling	tropical	1995	1996	165,000	32	302	0	no	1	42.702	2.60
488	Tam, J.	Northern Humboldt Current	upwelling	tropical	1997	1998	165,000	32	222	0	no	1	25.311	3.12
490	Taylor, M.H.	Independence Bay, Peru	bay / fjord	tropical	1996	1996	65.8	19	754	0	yes	1	12.605	2.73

No	Author	Location	Туре	Zone	Start	End	Area	Groups	Btot	Bestim	TS	Fleets	Ytot	TLY
491	Tomczak, M.T.	Gulf of Riga, SE Baltic Sea	bay / fjord	temperate	1990	1990	240	11	167	0	no	1	0.983	3.12
494	Tomczak, M.T.	Puck Bay, SE Baltic Sea	bay / fjord	temperate	1990	1990	359	11	362	0	no	1	1.180	3.02
495	Tsagarakis, K.	Aegean Sea, Northern	continental shelf	temperate	2003	2006	8,374	38	33	1	no	5	2.345	3.47
497	Valls, A.	Port-Cros National Park, SE France	continental shelf	temperate	1998	2008	13	40	9131	11	no	1	0.321	3.45
499	Wabnitz, C.C.	Kaloko- Honokohau, Honolulu, Hawaii	coral reef	tropical	2005	2005	2.48	25	700	1	no	2	0.347	2.59
500	Watermeyer, K	Benguela, Northern	upwelling	tropical	1600	1600	179,000	25	532	17	no	0	_	_
501	Watermeyer, K	Benguela, Northern	upwelling	tropical	1900	1900	179,000	25	485	17	no	2	0.002	4.42
502	Watermeyer, K.	Benguela, Northern	upwelling	tropical	1967	1967	179,000	25	501	17	no	4	9.295	3.20
503	Watermeyer, K.	Benguela, Northern	upwelling	tropical	1990	1990	179,000	25	621	14	no	8	2.826	3.68
504	Watermeyer, K.	Benguela, Southern	upwelling	temperate	1600	1600	220,000	31	234	23	no	0	_	_
505	Watermeyer, K.	Benguela, Southern	upwelling	temperate	1900	1900	220,000	31	220	23	no	2	0.020	4.52
506	Watermeyer,	Benguela, Southern	upwelling	temperate	1960	1960	220,000	31	191	20	no	4	2.716	3.56
507	Zhang, Y.	Gulf of Maine	continental shelf	temperate	1980	1980	103,000	23	300	0	no	0	_	_
508	Zhang, Y.	Gulf of Maine	continental shelf	temperate	1990	1990	103,000	23	487	0	no	0	_	_
522	Tecchio, S.	Catalan Sea	ocean	temperate	2009	2009	850	19	4	2	yes	0	_	_

Table C3. References of the 101 selected Ecopath models, with: model number in EcoBase (*No*); reference code in EcoBase (*ID*); first author(s) and year of publication (*Citation*); full reference as recorded in EcoBase (*Reference*).

No	ID	Citation	Reference
13	13	Ainsworth et al. 2001	Ainsworth, C., B. Feriss, E. Leblond, and S. Guénette. 2001. The Bay of Biscay, France: 1998 and 1970 models. Pages 271-313 in S. Guénette, V. Christensen, and D. Pauly, editors. Fisheries Impacts on North Atlantic Ecosystems: Models and Analyses. University of British Columbia, Vancouver, B.C., Canada.
14	13	Ainsworth et al. 2001	Ainsworth, C., B. Feriss, E. Leblond, and S. Guénette. 2001. The Bay of Biscay, France: 1998 and 1970 models. Pages 271-313 in S. Guénette, V. Christensen, and D. Pauly, editors. Fisheries Impacts on North Atlantic Ecosystems: Models and Analyses. University of British Columbia, Vancouver, B.C., Canada.
28	27	Vasconcellos and Watson 2004	Vasconcellos, M., and R. Watson. 2004. Mass-balance models of oceanic systems in the Atlantic. Pages 171-214 in M. L. D. Palomares and D. Pauly, editors. West African marine ecosystems: models and fisheries impacts. Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
29	27	Vasconcellos and Watson 2004	Vasconcellos, M., and R. Watson. 2004. Mass-balance models of oceanic systems in the Atlantic. Pages 171-214 in M. L. D. Palomares and D. Pauly, editors. West African marine ecosystems: models and fisheries impacts. Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
34	32	Christensen et al. 2009	Christensen, V., A. Beattie, C. Buchanan, M. Hongguang, S. J. Martell, R. J. Latour, D. Preikshot, M. B. Sigrist, J. Uphoff, C. Walters, R. Wood, and H. Townsend. 2009. Fisheries Ecosystem Model of the Chesapeake Bay: Methodology, Parameterization, and Model Exploration. NMFS-F/SPO-106, US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.
35	32	Christensen et al. 2009	Christensen, V., A. Beattie, C. Buchanan, M. Hongguang, S. J. Martell, R. J. Latour, D. Preikshot, M. B. Sigrist, J. Uphoff, C. Walters, R. Wood, and H. Townsend. 2009. Fisheries Ecosystem Model of the Chesapeake Bay: Methodology, Parameterization, and Model Exploration. NMFS-F/SPO-106, US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.
40	35	Bundy 2005	Bundy, A. 2005. Structure and functioning of the eastern Scotian Shelf ecosystem before and after the collapse of groundfish stocks in the early 1990s. Canadian Journal of Fisheries and Aquatic Sciences 62:1453-1473.
41	35	Bundy 2005	Bundy, A. 2005. Structure and functioning of the eastern Scotian Shelf ecosystem before and after the collapse of groundfish stocks in the early 1990s. Canadian Journal of Fisheries and Aquatic Sciences 62:1453-1473.
48	43	Okey et al. 2004	Okey, T. A., S. Banks, A. F. Born, R. H. Bustamante, M. Calvopiña, G. J. Edgar, E. Espinoza, J. M. Fariña, L. E. Garske, G. K. Reck, S. Salazar, S. Shepherd, V. Toral-Granda, and P. Wallem. 2004. A trophic model of a Galápagos subtidal rocky reef for evaluating fisheries and conservation strategies. Ecological Modelling 172:383-401.
49	44	Mendy 2004	Mendy, A. N. 2004. A trophic model of the Gambian continental shelf system in 1986. Pages 81-88 in M. L. D. Palomares and D. Pauly, editors. West African marine ecosystems: models and fisheries impacts. Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.

No	ID	Citation	Reference
50	45	Mendy 2004	Mendy, A. N. 2004. Addendum: The Gambian continental shelf ecosystem in 1992 and 1995. Pages 89-94 in M. L. D. Palomares and D. Pauly, editors. West African marine ecosystems: models and fisheries impacts. Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
51	45	Mendy 2004	Mendy, A. N. 2004. Addendum: The Gambian continental shelf ecosystem in 1992 and 1995. Pages 89-94 in M. L. D. Palomares and D. Pauly, editors. West African marine ecosystems: models and fisheries impacts. Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
55	50	Guénette and Diallo 2004	Guénette, S., and I. Diallo. 2004. Addendum: Modèles de la côte guinéenne, 1985 et 1998. Pages 124-159 in M. L. D. Palomares and D. Pauly, editors. West African marine ecosystems: models and fisheries impacts. Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
56	50	Guénette and Diallo 2004	Guénette, S., and I. Diallo. 2004. Addendum: Modèles de la côte guinéenne, 1985 et 1998. Pages 124-159 in M. L. D. Palomares and D. Pauly, editors. West African marine ecosystems: models and fisheries impacts. Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
66	60	Mendy and Buchary 2001	Mendy, A. N., and E. A. Buchary. 2001. Constructing an Icelandic marine ecosystem model for 1997 using a mass-balance modeling approach. Pages 182-197 in S. Guénette, V. Christensen, and D. Pauly, editors. Fisheries Impacts on North Atlantic Ecosystems: Models and Analyses. University of British Columbia, Vancouver, B.C., Canada.
96	85	Sidi and Guénette 2004	Ould Taleb Ould Sidi, M.M., and S. Guénette. 2004. Modèle trophique de la ZEE mauritanienne: comparaison de deux périodes (1987 et 1998). Pages 12-38 in M. L. D. Palomares and D. Pauly, editors. West African marine ecosystems: models and fisheries impacts. Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
97	85	Sidi and Guénette 2004	Ould Taleb Ould Sidi, M.M., and S. Guénette. 2004. Modèle trophique de la ZEE mauritanienne: comparaison de deux périodes (1987 et 1998). Pages 12-38 in M. L. D. Palomares and D. Pauly, editors. West African marine ecosystems: models and fisheries impacts. Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
98	86	Sidi and Samba 2004	Ould Taleb Ould Sidi, M.M., and D. M. Samba. 2004. Modèle écotrophique du Banc d'Arguin (Mauritanie) dans la période 1988 à 1998. Pages 4-11 in M. L. D. Palomares and D. Pauly, editors. West African marine ecosystems: models and fisheries impacts. Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
107	94	Heymans 2003	Heymans, J. J. 2003. Ecosystem models of Newfoundland and Southeastern Labrador: Additional information and analyses for 'Back to the Future'. 1198-6727, The Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
108	94	Heymans 2003	Heymans, J. J. 2003. Ecosystem models of Newfoundland and Southeastern Labrador: Additional information and analyses for 'Back to the Future'. 1198-6727, The Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.

No	ID	Citation	Reference
115	101	Heymans et al. 2009	Heymans, J. J., U. R. Sumaila, and V. Christensen. 2009. Policy options for the northern Benguela ecosystem using a multispecies, multifleet ecosystem model. Progress in Oceanography 83:417-425.
124	108	Jarre-Teichmann and Pauly 1993	Jarre-Teichmann, A., and D. Pauly. 1993. Seasonal Changes in the Peruvian Upwelling Ecosystem. Pages 307- 314 in Trophic models of aquatic ecosystems. ICLARM Conf. Proc.
135	119	Heymans and Vakily 2004	Heymans, J., and J. Vakily. 2004. Structure and dynamics of the marine ecosystem off Sierra Leone for three time periods: 1964, 1978, 1990. Pages 160-169 in M. L. D. Palomares and D. Pauly, editors. West African marine ecosystems: models and fisheries impacts. Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
136	119	Heymans and Vakily 2004	Heymans, J., and J. Vakily. 2004. Structure and dynamics of the marine ecosystem off Sierra Leone for three time periods: 1964, 1978, 1990. Pages 160-169 in M. L. D. Palomares and D. Pauly, editors. West African marine ecosystems: models and fisheries impacts. Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
137	119	Heymans and Vakily 2004	Heymans, J., and J. Vakily. 2004. Structure and dynamics of the marine ecosystem off Sierra Leone for three time periods: 1964, 1978, 1990. Pages 160-169 in M. L. D. Palomares and D. Pauly, editors. West African marine ecosystems: models and fisheries impacts. Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
145	124	Savenkoff et al. 2004	Savenkoff, C., H. Bourdages, D. P. Swain, SP. Despatie, J. M. Hanson, R. Méthot, L. Morissette, and M. O. Hammill. 2004. Input data and parameter estimates for ecosystem models of the southern Gulf of St. Lawrence (mid-1980s and mid-1990s). 0706-6457.
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195	159	Ainsworth et al. 2002	Ainsworth, C., J. J. Heymans, T. J. Pitcher, and M. Vasconcellos. 2002. Ecosystem Models of Northern British Columbia for the Time Periods 2000, 1950, 1900 and 1750. 1198-6727, The Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
196	159	Ainsworth et al. 2002	Ainsworth, C., J. J. Heymans, T. J. Pitcher, and M. Vasconcellos. 2002. Ecosystem Models of Northern British Columbia for the Time Periods 2000, 1950, 1900 and 1750. 1198-6727, The Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
197	159	Ainsworth et al. 2002	Ainsworth, C., J. J. Heymans, T. J. Pitcher, and M. Vasconcellos. 2002. Ecosystem Models of Northern British Columbia for the Time Periods 2000, 1950, 1900 and 1750. 1198-6727, The Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.

No	ID	Citation	Reference
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205	103	Morissette et al. 2003	Morissette, L., SP. Despatie, C. Savenkoff, M. O. Hammill, H. Bourdages, and D. Chabot. 2003. Data gathering and input parameters to construct ecosystem models for the northern Gulf of St. Lawrence (mid-1980's). 0706-6457, Department of Fisheries and Oceans, Quebec, Canada.
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208	28	Neira et al. 2004	Neira, S., H. Arancibia, and L. Cubillos. 2004. Comparative analysis of trophic structure of commercial fishery species off Central Chile in 1992 and 1998. Ecological Modelling 172:233-248.
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251	98	Christensen 1995	Christensen, V. 1995. A Model of Throphic Interactions in the North Sea in 1981, the Year of the Stomach. Dana 11:1-28.
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271	38	Stanford and Pitcher 2004	Stanford, R., and T. Pitcher. 2004. Ecosystem Simulations of the English Channel: Climate and Trade-Offs. 1198-6727, The Fisheries Centre, University of British Columbia, Vancouver, Canada.
272	38	Stanford and Pitcher 2004	Stanford, R., and T. Pitcher. 2004. Ecosystem Simulations of the English Channel: Climate and Trade-Offs. 1198-6727, The Fisheries Centre, University of British Columbia, Vancouver, Canada.
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No	ID	Citation	Reference
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293	99	Mackinson 2001	Mackinson, S. 2001. Representing trophic interactions in the North Sea in the 1880s, using the Ecopath mass- balance approach. Pages 35-98 in S. Guénette, V. Christensen, and D. Pauly, editors. Fisheries Impacts on North Atlantic Ecosystems: Models and Analyses. Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
294	57	Blanchard et al. 2002	Blanchard, J., J. Pinnegar, and S. Mackinson. 2002. Exploring Marine Mammal-Fishery Interactions Using 'Ecopath with Ecosim': Modelling the Barents Sea Ecosystem. Ministry of Agriculture, Fisheries and Food, Centre for Environment, Fisheries and Aquaculture Science, Lowestoft.
295	57	Blanchard et al. 2002	Blanchard, J., J. Pinnegar, and S. Mackinson. 2002. Exploring Marine Mammal-Fishery Interactions Using 'Ecopath with Ecosim': Modelling the Barents Sea Ecosystem. Ministry of Agriculture, Fisheries and Food, Centre for Environment, Fisheries and Aquaculture Science, Lowestoft.
297	152	Araújo et al. 2008	Araújo, J. N., S. Mackinson, R. J. Stanford, and P. J. Hart. 2008. Exploring fisheries strategies for the western English Channel using an ecosystem model. Ecological Modelling 210:465-477.
311	108	Jarre-Teichmann and Pauly 1993	Jarre-Teichmann, A., and D. Pauly. 1993. Seasonal Changes in the Peruvian Upwelling Ecosystem. Pages 307- 314 in Trophic models of aquatic ecosystems. ICLARM Conf. Proc.
312	108	Jarre-Teichmann and Pauly 1993	Jarre-Teichmann, A., and D. Pauly. 1993. Seasonal Changes in the Peruvian Upwelling Ecosystem. Pages 307- 314 in Trophic models of aquatic ecosystems. ICLARM Conf. Proc.
324	139	Opitz 1993	Opitz, S. 1993. A quantitative model of the trophic interactions in a Caribbean coral reef ecosystem. Pages 259-267 in Trophic models of aquatic ecosystems. ICLARM Conf. Proc.
328	128	Martell et al. 2002	Martell, S. J., A. I. Beattie, C. J. Walters, T. Nayar, and R. Briese. 2002. Simulating fisheries management strategies in the Strait of Georgia ecosystem using Ecopath and Ecosim. Pages 16-23 in T. Pitcher and K. Cochrane, editors. The Use of Ecosystem Models to Investigate Multispecies Management Strategies for Capture Fisheries. Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
400	301	Ainsworth et al. 2008	Ainsworth, C., D. Varkey, and T. Pitcher. 2008. Ecosystem simulations supporting ecosystem-based fisheries management in the Coral Triangle, Indonesia. Ecological Modelling 214:361-374.
401	301	Ainsworth et al. 2008	Ainsworth, C., D. Varkey, and T. Pitcher. 2008. Ecosystem simulations supporting ecosystem-based fisheries management in the Coral Triangle, Indonesia. Ecological Modelling 214:361-374.
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No	ID	Citation	Reference
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412	56	Christensen 1998	Christensen, V. 1998. Fishery-induced changes in a marine ecosystem: insight from models of the Gulf of Thailand. Journal of Fish Biology 53:128-142.
413	317	Christensen et al. 2002	Christensen, V., G. Reck, and J. L. Maclean. 2002. Proceedings of the INCO-DC Conference Placing Fisheries in their Ecosystem Context. Page 79 in Fisheries Research Report. ACP-EU, Galapagos Islands, Ecuador.
418	321	Coll et al. 2006	Coll, M., I. Palomera, S. Tudela, and F. Sardà. 2006. Trophic flows, ecosystem structure and fishing impacts in the South Catalan Sea, Northwestern Mediterranean. Journal of Marine Systems 59:63-96.
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420	323	Coll et al. 2008	Coll, M., I. Palomera, S. Tudela, and M. Dowd. 2008. Food-web dynamics in the South Catalan Sea ecosystem (NW Mediterranean) for 1978–2003. Ecological Modelling 217:95-116.
421	324	Coll et al. 2009	Coll, M., A. Santojanni, I. Palomera, and E. Arneri. 2009. Food-web changes in the Adriatic Sea over the last three decades. Marine Ecology Progress Series 381:17-37.
427	331	Erfan and Pitcher 2005	Erfan, A., and T. J. Pitcher. 2005. An Ecosystem Simulation Model of the Antarctic Peninsula. Pages 5-20 in M. L. D. Palomares, P. Pruvost, T. J. Pitcher, and D. Pauly, editors. Modeling Antarctic Marine Ecosystems. Fisheries Centre, Vancouver, B.C., Canada.
429	333	Falk-Petersen 2004	Falk-Petersen, J. 2004. Ecosystem effects of red king crab invasion - a modelling approach using Ecopath with Ecosim. University of Tromso, Tromso, Norway.
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442	346	Heymans 2005	Heymans, J. J. 2005. Ecosystem model of the eastern Aleutians and central Gulf of Alaska in 1963. Pages 83-105 in S. Guenette and V. Christensen, editors. Food web models and data for studying fisheries and environmental impacts on Eastern Pacific ecosystems. Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
444	345	Heymans 2001	Heymans, J. J. 2001. The Gulf of Maine, 1977-1986. Pages 129-149 in S. Guénette, V. Christensen, and D. Pauly, editors. Fisheries Impacts on North Atlantic Ecosystems: Models and Analyses. Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
450	356	Lercari and Arreguín-Sánchez 2009	Lercari, D., and F. Arreguín-Sánchez. 2009. An ecosystem modelling approach to deriving viable harvest strategies for multispecies management of the Northern Gulf of California. Aquatic Conservation: Marine and Freshwater Ecosystems 19:384-397.

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452	358	Libralato et al. 2010	Libralato, S., M. Coll, M. Tempesta, A. Santojanni, M. Spoto, I. Palomera, E. Arneri, and C. Solidoro. 2010. Food-web traits of protected and exploited areas of the Adriatic Sea. Biological Conservation 143:2182-2194.
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485	389	Shannon et al. 2004	Shannon, L., V. Christensen, and C. Walters. 2004. Modelling stock dynamics in the southern Benguela ecosystem for the period 1978–2002. African Journal of Marine Science 26:179-196.
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No	ID	Citation	Reference
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501	406	Watermeyer et al. 2008a	Watermeyer, K., L. Shannon, J. Roux, and C. Griffiths. 2008. Changes in the trophic structure of the northern Benguela before and after the onset of industrial fishing. African Journal of Marine Science 30:383-403.
502	406	Watermeyer et al. 2008a	Watermeyer, K., L. Shannon, J. Roux, and C. Griffiths. 2008. Changes in the trophic structure of the northern Benguela before and after the onset of industrial fishing. African Journal of Marine Science 30:383-403.
503	406	Watermeyer et al. 2008a	Watermeyer, K., L. Shannon, J. Roux, and C. Griffiths. 2008. Changes in the trophic structure of the northern Benguela before and after the onset of industrial fishing. African Journal of Marine Science 30:383-403.
504	407	Watermeyer et al. 2008b	Watermeyer, K., L. Shannon, and C. Griffiths. 2008. Changes in the trophic structure of the southern Benguela before and after the onset of industrial fishing. African Journal of Marine Science 30:351-382.
505	407	Watermeyer et al. 2008b	Watermeyer, K., L. Shannon, and C. Griffiths. 2008. Changes in the trophic structure of the southern Benguela before and after the onset of industrial fishing. African Journal of Marine Science 30:351-382.
506	407	Watermeyer et al. 2008b	Watermeyer, K., L. Shannon, and C. Griffiths. 2008. Changes in the trophic structure of the southern Benguela before and after the onset of industrial fishing. African Journal of Marine Science 30:351-382.
507	409	Zhang and Chen 2007	Zhang, Y., and Y. Chen. 2007. Modeling and evaluating ecosystem in 1980s and 1990s for American lobster (<i>Homarus americanus</i>) in the Gulf of Maine. Ecological Modelling 203:475-489.

No	ID	Citation	Reference
508	409	Zhang and Chen 2007	Zhang, Y., and Y. Chen. 2007. Modeling and evaluating ecosystem in 1980s and 1990s for American lobster (<i>Homarus americanus</i>) in the Gulf of Maine. Ecological Modelling 203:475-489.
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Table C4. Detailed results for the selected index of keystoneness (KS_3) and the 101 selected Ecopath models, with: model number (No); name of highest keystoneness group with selected KS index (*First Group*); matching between groups ordered by selected KS index and by trophic impact or biomass (*Match*); validation of rank correlation tests (*Correlation*); categorization of highest keystoneness group with selected KS index as Keystone with classification tree (*KS Category*); allocation of model status (*Status*).

No	First Group	Match	Correlation	KS Category	Status
13	LargeSharks	MatchImpact	Yes	No	FalsePositive
14	LargeSharks	MatchImpact	Yes	No	FalsePositive
28	Pelagicsharks	MatchImpact	Yes	No	FalsePositive
29	AllFleets	MatchImpact	Yes	No	FalsePositive
34	Piscivorousbirds	NoMatch	Yes	Yes	TruePositive
35	Piscivorousbirds	NoMatch	No	Yes	FalseNegative
40	LargeCrabs	NoMatch	Yes	Yes	TruePositive
41	AllFleets	MatchImpact	Yes	No	FalsePositive
48	Sharks	MatchBiomass	No	Yes	FalseNegative
49	Sharks	MatchImpact	Yes	NA	NoKeystone
50	Sharks	MatchImpact	Yes	NA	NoKeystone
51	Sharks	MatchImpact	Yes	NA	NoKeystone
55	Sharks	MatchImpact	No	Yes	FalseNegative
56	SelaciensLcotiers	MatchImpact	Yes	No	FalsePositive
66	Baleenwhales	NoMatch	Yes	NA	TruePositive
96	demLpred	MatchImpact	Yes	Yes	TruePositive
97	demLpred	MatchImpact	Yes	NA	NoKeystone
98	AllFleets	MatchImpact	Yes	NA	NoKeystone
107	Cetaceans	NoMatch	Yes	No	FalsePositive
108	AllFleets	MatchImpact	Yes	NA	FalsePositive
115	Benthicproducers	MatchImpact	No	NA	NoKeystone
124	AllFleets	MatchImpact	Yes	NA	NoKeystone
135	MCoastalSharksandRays	MatchImpact	No	NA	NoKeystone
136	LCoastalSharksandRays	MatchBiomass	Yes	Yes	TruePositive
137	LCoastalSharksandRays	NoMatch	Yes	Yes	TruePositive
145	Largedemersalfeeders	NoMatch	Yes	NA	NoKeystone
182	AllFleets	MatchImpact	Yes	NA	NoKeystone
194	Odontocetae	MatchImpact	No	Yes	FalseNegative
195	Odontocetae	MatchImpact	No	Yes	FalseNegative
196	Commercialshrimp	MatchImpact	No	Yes	FalseNegative
197	Transientsalmon	MatchImpact	No	No	TrueNegative
202	AllFleets	MatchImpact	Yes	No	FalsePositive
205	AllFleets	MatchImpact	Yes	NA	NoKeystone
207	Sealion	MatchBiomass	Yes	Yes	TruePositive
208	AllFleets	MatchImpact	No	NA	NoKeystone

No	First Group	Match	Correlation	KS Category	Status
227	Herring	MatchImpact	Yes	NA	NoKeystone
239	SharksRays	MatchImpact	Yes	Yes	TruePositive
251	AllFleets	MatchImpact	No	NA	NoKeystone
252	Transientorca	MatchBiomass	No	Yes	FalseNegative
254	Bluemarlin	MatchBiomass	Yes	Yes	TruePositive
271	Seals	MatchBiomass	No	Yes	FalseNegative
272	Bass	NoMatch	No	Yes	FalseNegative
276	AllFleets	MatchImpact	Yes	NA	NoKeystone
277	Toothedwhales	MatchImpact	Yes	Yes	TruePositive
293	AllFleets	MatchImpact	No	No	TrueNegative
294	Sharks	MatchBiomass	Yes	Yes	TruePositive
295	Sharks	MatchImpact	Yes	Yes	TruePositive
297	Sharks	MatchBiomass	Yes	Yes	TruePositive
311	AllFleets	MatchImpact	Yes	NA	NoKeystone
312	Cormorant	NoMatch	Yes	NA	NoKeystone
324	F1SharksRays	MatchBiomass	Yes	Yes	TruePositive
328	Transientorcas	MatchBiomass	Yes	Yes	TruePositive
400	Adultlargesharks	MatchImpact	No	Yes	FalseNegative
401	Adultlargesharks	MatchImpact	No	Yes	FalseNegative
402	AllFleets	MatchImpact	Yes	Yes	TruePositive
407	Alepocephalids	NoMatch	No	NA	FalseNegative
410	Pelagicsharksandrays	MatchImpact	Yes	Yes	TruePositive
412	Mmammals	NoMatch	Yes	Yes	TruePositive
413	AllFleets	MatchImpact	No	NA	NoKeystone
418	Audouinsgull	MatchBiomass	Yes	NA	TruePositive
419	Dolphins	NoMatch	Yes	Yes	TruePositive
420	Audouinsgull	MatchBiomass	Yes	NA	TruePositive
421	Dolphins	MatchBiomass	Yes	Yes	TruePositive
427	toothedwhales	MatchBiomass	Yes	Yes	TruePositive
429	AllFleets	MatchImpact	Yes	No	FalsePositive
433	AllFleets	MatchBiomass	No	NA	NoKeystone
434	AllFleets	MatchImpact	Yes	NA	NoKeystone
435	AllFleets	MatchBiomass	Yes	NA	NoKeystone
442	Transientorca	MatchBiomass	No	Yes	FalseNegative
444	Herring	MatchImpact	Yes	NA	NoKeystone
450	Elasmobranchssharks	MatchImpact	Yes	No	FalsePositive
451	demersalfishes2	NoMatch	Yes	NA	NoKeystone
452	mesozooplancton	MatchImpact	No	NA	NoKeystone
454	piscovorousfish	MatchImpact	Yes	NA	NoKeystone
457	Largepiscivoroussharks	MatchBiomass	Yes	Yes	TruePositive
458	TransOrcas	MatchBiomass	Yes	Yes	TruePositive
462	Harpseals	MatchImpact	Yes	No	FalsePositive

No	irst GroupMatchCorrelationKS Category		Status		
472	mobileinvcarn	MatchImpact	Yes	Yes	TruePositive
474	Bottlenosedolphins	NoMatch	Yes	Yes	TruePositive
475	Bottlenosedolphins	NoMatch	Yes	NA	NoKeystone
482	pelagicsharks	MatchBiomass	Yes	Yes	TruePositive
483	pelagicsharks	MatchImpact	Yes	Yes	TruePositive
485	Snoek	NoMatch	Yes	Yes	TruePositive
487	largehake	NoMatch	Yes	Yes	TruePositive
488	butterfishes	MatchBiomass	Yes	NA	TruePositive
490	smallpelagicfish	NoMatch	Yes	NA	NoKeystone
491	Piscivorousfish	MatchImpact	Yes	NA	NoKeystone
494	Piscivorousfish	MatchBiomass	Yes	NA	NoKeystone
495	Benthopelagiccephalopods	NoMatch	No	NA	NoKeystone
497	AllFleets	NoMatch	Yes	NA	NoKeystone
499	Sharksandjacks	MatchBiomass	Yes	Yes	TruePositive
500	Cetaceans	MatchBiomass	Yes	Yes	TruePositive
501	Seals	MatchBiomass	Yes	Yes	TruePositive
502	Cetaceans	MatchBiomass	Yes	Yes	TruePositive
503	Largepelagics	MatchImpact	Yes	Yes	TruePositive
504	Apexchond	MatchBiomass	Yes	Yes	TruePositive
505	Apexchondricht	NoMatch	Yes	Yes	TruePositive
506	Apexchondricht	MatchBiomass	Yes	Yes	TruePositive
507	adultlobster	NoMatch	No	NA	NoKeystone
508	otherfishes	MatchImpact	No	NA	NoKeystone
522	Zooplanktongelatinous	NoMatch	No	NA	FalseNegative

Appendix D: Weighted averaged diet percent calculated based on FishBase diet data

Table D1. List of the 501 weighted averaged diet percent (WADP) and associated standard error of the mean (*SEM*), calculated based on diet information available in FishBase, for each pair of predator-prey species selected for the analyses. The 132 WADP selected for the analyses are highlighted in bold.

Code	Predator	Prey	WADP	SEM		Code	Predator	Prey	WADP	SEM
1	28	23	69.5	1.51	-	32	29	716	3.2	0.00
2	28	24	100.0	2.17		33	29	754	19.7	0.04
3	28	29	65.5	2.82		34	29	1023	51.3	0.56
4	28	69	85.9	3.24		35	29	1327	3.6	0.00
5	28	1023	80.5	10.50		36	29	1341	100.0	0.03
6	28	1367	100.0	2.14		37	29	1343	8.0	0.00
7	28	1381	100.0	3.09		38	29	1345	9.6	0.01
8	28	4239	28.5	0.84		39	29	1352	15.4	0.01
9	29	22	40.5	0.01		40	29	1357	36.5	0.28
10	29	23	8.8	0.01		41	29	1359	1.8	0.00
11	29	24	37.0	0.21		42	29	1364	29.8	0.02
12	29	26	4.8	0.00		43	29	1365	22.7	0.06
13	29	28	25.0	0.01		44	29	1367	21.9	0.01
14	29	29	28.0	0.18		45	29	1374	28.3	0.04
15	29	30	15.3	0.01		46	29	1380	6.4	0.00
16	29	31	40.5	0.02		47	29	1381	26.6	0.14
17	29	35	39.5	0.01		48	29	1382	0.6	0.00
18	29	36	6.8	0.00		49	29	1770	1.0	0.00
19	29	37	31.0	0.14		50	29	1875	39.4	0.06
20	29	38	27.2	0.03		51	29	2501	9.8	0.01
21	29	41	3.3	0.00		52	29	2513	30.1	0.01
22	29	47	59.1	0.02		53	29	4239	18.9	0.05
23	29	53	21.4	0.03		54	29	15761	16.0	0.01
24	29	60	9.8	0.01		55	30	24	86.0	5.46
25	29	65	9.5	0.00		56	30	29	49.6	1.96
26	29	69	16.0	0.04		57	30	53	1.2	0.01
27	29	75	58.1	0.02		58	30	118	84.8	1.10
28	29	118	22.9	0.02		59	30	481	100.0	0.92
29	29	481	17.6	0.02		60	30	695	14.6	0.32
30	29	525	21.5	0.02		61	30	1023	83.4	4.68
31	29	695	6.2	0.01		62	30	1357	100.0	0.92

Code	Predator	Prey	WADP	SEM	Code	Predator	Prey	WADP	SEM
63	30	1374	11.4	0.17	103	68	1023	44.0	0.87
64	30	1381	35.3	0.63	104	68	1329	0.6	0.00
65	30	4239	68.1	1.40	105	68	1342	34.4	0.06
66	30	15761	100.0	0.91	106	68	1343	38.8	0.07
67	33	24	38.4	3.98	107	68	1357	30.8	0.25
68	33	29	67.2	6.65	108	68	1360	12.6	0.02
69	33	69	100.0	7.08	109	68	1365	21.8	0.06
70	33	118	94.4	4.61	110	68	1367	26.8	0.08
71	33	1023	76.3	10.27	111	68	1374	48.4	0.32
72	33	1381	100.0	8.67	112	68	1378	4.8	0.01
73	33	15761	71.1	4.90	113	68	1381	44.5	0.32
74	34	24	33.9	2.34	114	68	1807	23.0	0.10
75	34	29	27.6	2.85	115	68	2059	100.0	0.18
76	34	69	100.0	10.81	116	68	2501	28.0	0.12
77	34	1023	96.5	17.25	117	68	3804	1.1	0.00
78	34	1365	88.6	6.13	118	68	4239	14.3	0.26
79	34	1381	35.8	4.42	119	69	22	7.0	0.01
80	34	15761	100.0	7.82	120	69	23	7.4	0.03
81	44	76	35.2	13.49	121	69	24	16.7	0.09
82	44	1807	44.6	13.90	122	69	26	9.3	0.01
83	51	24	100.0	26.02	123	69	28	7.2	0.00
84	51	69	100.0	25.26	124	69	29	17.4	0.10
85	51	4239	100.0	25.26	125	69	31	98.8	0.02
86	68	22	21.0	0.24	126	69	33	9.9	0.00
87	68	23	21.5	0.30	127	69	34	77.8	0.02
88	68	24	22.5	0.12	128	69	35	11.7	0.00
89	68	26	13.5	0.06	129	69	36	2.3	0.00
90	68	29	28.3	0.52	130	69	38	63.2	0.02
91	68	31	100.0	0.18	131	69	39	2.1	0.00
92	68	36	4.8	0.02	132	69	41	1.9	0.00
93	68	39	13.7	0.03	133	69	45	39.6	0.01
94	68	41	22.9	0.08	134	69	47	28.0	0.01
95	68	53	11.6	0.06	135	69	53	4.0	0.01
96	68	60	38.4	0.07	136	69	60	2.9	0.00
97	68	68	13.9	0.03	137	69	66	4.9	0.00
98	68	69	32.6	0.52	138	69	68	4.2	0.00
99	68	118	22.5	0.09	139	69	69	13.9	0.04
100	68	481	58.8	0.26	140	69	76	4.7	0.00
101	68	525	47.0	0.09	141	69	118	17.1	0.02
102	68	695	13.8	0.23	142	69	479	2.0	0.00

Code	Predator	Prey	WADP	SEM	Code	Predator	Prey	WADP	SEM
143	69	481	9.2	0.01	183	69	15761	8.3	0.01
144	69	525	6.2	0.01	184	118	23	9.6	0.07
145	69	529	0.5	0.00	185	118	24	41.8	0.63
146	69	643	1.9	0.00	186	118	26	0.6	0.00
147	69	695	13.3	0.08	187	118	29	74.0	0.30
148	69	754	15.3	0.02	188	118	31	23.4	0.11
149	69	845	12.8	0.00	189	118	38	76.7	0.46
150	69	1023	31.9	0.20	190	118	39	0.2	0.00
151	69	1329	4.4	0.00	191	118	41	0.3	0.00
152	69	1334	8.7	0.00	192	118	69	27.7	0.23
153	69	1341	14.4	0.01	193	118	118	4.6	0.07
154	69	1342	5.9	0.01	194	118	481	12.0	0.05
155	69	1343	79.9	0.03	195	118	695	6.3	0.03
156	69	1345	5.0	0.00	196	118	754	8.9	0.07
157	69	1348	2.4	0.00	197	118	1023	43.1	0.99
158	69	1352	24.3	0.01	198	118	1342	16.3	0.07
159	69	1357	11.7	0.04	199	118	1345	87.1	0.14
160	69	1364	1.2	0.00	200	118	1357	30.9	0.56
161	69	1365	11.1	0.01	201	118	1359	20.9	0.10
162	69	1366	3.5	0.00	202	118	1361	100.0	0.17
163	69	1367	6.3	0.01	203	118	1364	100.0	0.24
164	69	1369	83.9	0.01	204	118	1365	26.1	0.33
165	69	1374	12.8	0.02	205	118	1371	0.1	0.00
166	69	1378	6.1	0.00	206	118	1374	100.0	0.17
167	69	1380	10.5	0.01	207	118	1381	13.8	0.05
168	69	1381	23.3	0.12	208	118	1875	100.0	0.17
169	69	1382	15.7	0.01	209	118	2501	13.4	0.02
170	69	1383	8.4	0.00	210	139	22	41.6	0.35
171	69	1807	15.0	0.01	211	139	23	8.6	0.22
172	69	1875	62.0	0.01	212	139	24	33.3	2.27
173	69	1876	11.6	0.00	213	139	29	31.1	1.07
174	69	2059	29.8	0.01	214	139	38	13.1	0.37
175	69	2360	1.3	0.00	215	139	47	20.6	0.25
176	69	2501	10.0	0.01	216	139	53	4.1	0.09
177	69	2513	10.9	0.00	217	139	69	9.8	0.15
178	69	2700	20.2	0.01	218	139	118	29.4	0.84
179	69	3265	13.4	0.00	219	139	481	48.8	0.71
180	69	3804	7.1	0.00	220	139	525	34.3	0.40
181	69	4146	7.1	0.00	221	139	695	21.2	0.81
182	69	4239	11.7	0.07	222	139	1023	38.9	0.93

Code	Predator	Prey	WADP	SEM	Code	Predator	Prey	WADP	SEM
223	139	1342	50.1	0.59	263	716	33	100.0	0.83
224	139	1343	57.5	0.48	264	716	36	36.7	0.30
225	139	1357	13.5	0.35	265	716	68	100.0	0.82
226	139	1364	17.5	0.15	266	716	69	54.7	1.17
227	139	1365	14.6	0.17	267	716	118	72.7	1.20
228	139	1374	18.7	0.38	268	716	481	12.0	0.17
229	139	1380	100.0	0.84	269	716	695	49.4	1.34
230	139	1381	33.0	0.39	270	716	1023	29.1	1.45
231	139	2700	52.3	0.44	271	716	1342	69.6	1.51
232	139	3804	6.2	0.05	272	716	1367	100.0	0.83
233	139	4239	29.9	0.36	273	716	1381	60.7	2.12
234	139	9198	34.0	0.29	274	716	1875	6.8	0.05
235	481	754	38.9	25.11	275	716	2528	6.4	0.05
236	529	23	8.2	0.37	276	716	4239	48.3	1.59
237	529	24	14.7	0.66	277	716	15761	93.8	0.77
238	529	28	37.5	0.48	278	1023	24	31.3	1.95
239	529	29	34.3	2.04	279	1023	39	90.0	5.74
240	529	36	0.7	0.01	280	1023	60	39.8	3.17
241	529	45	69.1	0.88	281	1023	754	57.1	9.38
242	529	53	8.0	0.19	282	1023	1023	50.0	3.00
243	529	68	5.4	0.10	283	1023	1357	8.6	0.74
244	529	69	11.5	0.32	284	1023	1875	76.8	6.75
245	529	481	33.9	0.83	285	1023	3804	0.9	0.05
246	529	525	1.1	0.02	286	1343	24	30.8	0.29
247	529	695	4.9	0.32	287	1343	26	0.6	0.00
248	529	1023	100.0	1.27	288	1343	29	6.0	0.04
249	529	1329	21.2	0.27	289	1343	31	11.8	0.06
250	529	1342	100.0	1.27	290	1343	37	0.9	0.00
251	529	1345	3.6	0.06	291	1343	65	5.8	0.00
252	529	1357	3.8	0.18	292	1343	69	20.3	0.05
253	529	1364	19.7	0.70	293	1343	118	36.2	0.07
254	529	1365	9.8	0.31	294	1343	481	20.1	0.05
255	529	1366	1.0	0.01	295	1343	695	6.5	0.01
256	529	1367	6.6	0.13	296	1343	754	32.4	0.43
257	529	1374	100.0	1.80	297	1343	1023	37.3	0.93
258	529	4239	7.5	0.17	298	1343	1357	6.8	0.02
259	716	23	100.0	1.43	299	1343	1366	23.1	0.02
260	716	24	83.8	2.49	300	1343	1373	64.7	0.30
261	716	26	100.0	1.65	301	1343	1374	18.2	0.03
262	716	29	68.2	3.22	302	1343	1381	17.6	0.25

Code	Predator	Prey	WADP	SEM	Code	Predator	Prey	WADP	SEM
303	1343	1382	0.0	0.00	343	1365	39	18.9	0.59
304	1343	1875	3.9	0.03	344	1365	53	0.6	0.00
305	1343	2501	0.7	0.00	345	1365	60	24.0	0.34
306	1343	4239	1.7	0.01	346	1365	68	1.4	0.02
307	1343	15761	1.9	0.00	347	1365	481	6.4	0.05
308	1348	22	54.9	0.27	348	1365	695	15.4	0.39
309	1348	23	10.3	0.29	349	1365	1023	86.8	2.23
310	1348	24	15.8	0.46	350	1365	1329	2.7	0.02
311	1348	26	100.0	0.49	351	1365	1344	0.8	0.01
312	1348	28	2.1	0.01	352	1365	1345	8.6	0.12
313	1348	29	50.4	2.28	353	1365	1347	0.5	0.01
314	1348	36	1.0	0.01	354	1365	1348	0.3	0.00
315	1348	38	9.3	0.08	355	1365	1350	38.8	0.77
316	1348	41	19.3	0.09	356	1365	1357	39.9	1.55
317	1348	45	38.7	0.19	357	1365	1359	8.1	0.07
318	1348	53	3.4	0.07	358	1365	1363	9.2	0.10
319	1348	60	100.0	0.49	359	1365	1365	21.3	1.00
320	1348	68	3.4	0.05	360	1365	1367	0.2	0.00
321	1348	69	7.4	0.24	361	1365	1381	42.3	0.49
322	1348	118	6.4	0.03	362	1365	1382	0.4	0.01
323	1348	481	5.9	0.09	363	1365	1770	6.0	0.05
324	1348	525	3.8	0.03	364	1365	2360	0.2	0.00
325	1348	695	9.8	0.46	365	1365	4239	8.8	0.10
326	1348	1023	1.8	0.01	366	1366	22	36.5	1.58
327	1348	1342	8.2	0.07	367	1366	23	28.7	1.90
328	1348	1348	2.8	0.02	368	1366	29	45.4	1.69
329	1348	1357	19.0	0.48	369	1366	53	25.5	1.17
330	1348	1364	8.2	0.13	370	1366	69	84.1	0.95
331	1348	1365	1.1	0.02	371	1366	525	42.4	0.47
332	1348	1366	4.3	0.07	372	1366	695	25.6	1.57
333	1348	1367	6.5	0.12	373	1366	1023	27.9	0.31
334	1348	1381	8.3	0.16	374	1366	1342	100.0	1.13
335	1348	4239	6.6	0.15	375	1366	1365	20.8	0.23
336	1348	5355	8.7	0.04	376	1366	1366	14.3	0.16
337	1348	15761	27.1	0.13	377	1366	1807	31.8	0.50
338	1365	23	3.9	0.15	378	1366	4239	15.9	0.36
339	1365	24	57.5	2.03	379	1367	23	19.5	3.55
340	1365	26	0.3	0.00	380	1367	24	2.2	0.14
341	1365	29	66.8	2.35	381	1367	29	47.8	2.38
342	1365	38	0.6	0.01	382	1367	53	12.9	1.49

Code	Predator	Prey	WADP	SEM	Code	Predator	Prey	WADP	SEM
383	1367	481	11.7	0.85	423	2059	481	27.9	2.22
384	1367	1357	26.5	1.32	424	2059	525	60.1	5.17
385	1367	1374	41.5	3.09	425	2059	1342	20.3	1.40
386	1367	1875	3.6	0.18	426	2059	1357	21.8	3.25
387	1371	29	43.6	10.27	427	2059	1361	31.2	3.39
388	1371	1023	71.0	35.54	428	2059	3804	11.6	1.11
389	1374	24	29.0	8.28	429	2501	24	7.8	1.63
390	1374	29	89.7	24.67	430	2501	1023	32.4	16.16
391	1374	1357	100.0	28.53	431	2565	23	18.2	0.25
392	1374	1374	43.0	0.88	432	2565	24	26.9	0.43
393	1381	23	16.5	0.06	433	2565	26	15.4	0.18
394	1381	24	37.3	0.12	434	2565	29	22.6	0.52
395	1381	26	11.4	0.02	435	2565	33	100.0	0.82
396	1381	29	19.8	0.05	436	2565	36	29.5	0.34
397	1381	32	26.3	0.06	437	2565	37	76.0	0.62
398	1381	34	8.2	0.02	438	2565	38	86.1	0.98
399	1381	37	41.8	0.91	439	2565	41	100.0	0.82
400	1381	38	67.2	0.94	440	2565	68	30.6	0.25
401	1381	39	27.4	0.06	441	2565	69	22.1	0.44
402	1381	68	4.8	0.01	442	2565	481	13.5	0.11
403	1381	69	12.1	0.02	443	2565	525	92.8	0.76
404	1381	76	5.4	0.01	444	2565	695	26.9	0.73
405	1381	525	11.4	0.04	445	2565	754	19.7	0.16
406	1381	695	24.3	0.04	446	2565	1023	37.0	2.20
407	1381	754	41.7	0.10	447	2565	1329	100.0	0.82
408	1381	1023	50.6	0.93	448	2565	1345	29.0	0.24
409	1381	1342	1.2	0.00	449	2565	1357	49.8	0.57
410	1381	1343	15.0	0.02	450	2565	1367	34.1	0.27
411	1381	1346	2.5	0.00	451	2565	1371	16.8	0.14
412	1381	1357	34.4	0.24	452	2565	1374	34.4	0.27
413	1381	1374	47.1	0.21	453	2565	1380	37.3	0.30
414	1381	1381	46.8	0.22	454	2565	1381	83.7	1.36
415	1381	1875	3.1	0.01	455	2565	1807	35.0	0.70
416	1381	2501	13.2	0.02	456	2565	2360	5.2	0.04
417	1381	4239	16.3	0.16	457	2565	3804	4.2	0.03
418	2058	1374	100.0	0.00	458	2565	4239	19.4	0.74
419	2059	24	14.0	1.91	459	4239	23	24.3	0.33
420	2059	29	11.7	0.77	460	4239	24	100.0	0.97
421	2059	36	12.1	0.73	461	4239	29	58.7	2.66
422	2059	38	37.2	4.53	462	4239	39	100.0	0.97

Code	Predator	Prey	WADP	SEM
463	4239	68	9.6	0.18
464	4239	69	34.3	1.24
465	4239	1023	65.0	4.82
466	4239	1357	5.0	0.05
467	4239	1381	49.0	1.42
468	4239	2501	3.6	0.03
469	4239	3804	4.7	0.05
470	4239	4239	7.1	0.19
471	4326	22	87.6	9.30
472	4326	23	57.7	9.86
473	4326	24	80.7	7.61
474	4326	29	57.2	6.29
475	4326	72	11.1	1.05
476	4326	525	86.8	9.89
477	4326	1023	64.5	10.22
478	4329	38	12.5	1.38
479	4329	481	66.1	11.26
480	4329	1023	28.7	3.39
481	4329	1357	63.6	14.43
482	4329	1374	96.8	12.62
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Code	Predator	Prey	WADP	SEM
483	4329	1381	66.3	7.82
484	4642	23	18.2	1.82
485	4642	24	66.8	8.22
486	4642	29	33.5	2.52
487	4642	35	12.5	0.63
488	4642	36	2.7	0.06
489	4642	47	51.0	1.89
490	4642	69	14.9	0.73
491	4642	118	35.7	3.26
492	4642	481	5.3	0.19
493	4642	525	25.5	0.94
494	4642	695	10.8	0.69
495	4642	1023	5.5	0.20
496	4642	1342	51.6	2.70
497	4642	1357	8.9	0.66
498	4642	1365	12.0	0.80
499	4642	1367	52.6	1.97
500	4642	1381	21.5	0.81
501	4642	2700	77.5	2.83

Appendix E: Selection of biological and ecological parameters from FishBase

Table E1. List of biological and ecological parameters selected for predator and prey species, with associated acronym (in alphabetical order), and corresponding field, table and definition in FishBase.

Acronym	FishBase field(s)	FishBase table	FishBase definition
AAR	AspectRatio	MORPHOLOGY (MORPHMET)	Caudal Height * Caudal Height / Surface area of caudal fin
AFN	Afinno	MORPHOLOGY (MORPHDAT)	_
BN	BarbelsNo	MORPHOLOGY (MORPHDAT)	_
BS	BodyShapeI	MORPHOLOGY (MORPHDAT)	Shape of body in lateral view
CS	CShape	MORPHOLOGY (MORPHDAT)	_
D	Dangerous	SPECIES	Is this species poisnous or harmful?
DA	DorsalAttributes	MORPHOLOGY (MORPHDAT)	Striking attributes of dorsal fin
DFN	Dfinno	MORPHOLOGY (MORPHDAT)	_
DRD	DepthRangeDeep	SPECIES	Deepest occurrence of the species in meters
DSMa	DorsalSpinesMax	MORPHOLOGY (MORPHDAT)	Total number of spines in all dorsal fins
DSMi	DorsalSpinesMin	MORPHOLOGY (MORPHDAT)	Total number of spines in all dorsal fins
EsT	Saltwater + Brack + Fresh	SPECIES	Does the species occur in freshwater and/or brackish water and/or marine or hypersaline environments?
ET	DemersPelag	SPECIES	Environment preferred by species
FS	Forehead	MORPHOLOGY (MORPHDAT)	Shape of forehead in lateral view
FWHT	Estuaries + Lakes + Stream	ECOLOGY	Occurs in estuaries and/or lakes and/or stream
НТ	Oceanic + Neritic + Intertidal	ECOLOGY	Occurs in open/high seas and/or continental shelves and/or the littoral zone (area between tide marks)
KN	Keels	MORPHOLOGY (MORPHDAT)	_
ML	Length	SPECIES	Length of largest male or unsexed specimen ever caught
MP	PosofMouth	MORPHOLOGY (MORPHDAT)	_

Acronym	FishBase field(s)	FishBase table	FishBase definition
PA	PelvicsAttributes	MORPHOLOGY (MORPHDAT)	Striking attributes of pelvic fins
SA	Scutes + BarbelsType	MORPHOLOGY (MORPHDAT)	_
SF	StrikingFeatures	MORPHOLOGY (MORPHDAT)	_
SM	AdultMode	Swimming	_
VP	VPosition	MORPHOLOGY (MORPHDAT)	_
VP2	VPosition2	MORPHOLOGY (MORPHDAT)	