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Resumo

Ao longo dos tempos, a ineficiência da gestão pesqueira, promoveu a necessidade de melhorar ferramentas e metodologias de gestão, o que levou ao desenvolvimento de metodologias sofisticadas de modelação ecossistémica, que abrangem uma ampla gama de fatores bióticos e abióticos. Estes modelos enquadram-se globalmente em uma de duas categorias: modelos baseados em tamanhos e modelos de balanço de massa baseados na cadeia alimentar.

Os modelos de espectro de tamanho, que usam o tamanho como componente estruturante, ganharam popularidade nos últimos anos. Estes modelos, menos exigentes em termos de dados, quando comparados com outros, provaram ser eficazes para prever os efeitos de impactos ecossistémicos, como a pesca e as mudanças climáticas. De uma forma geral, os modelos enquadram-se em três categorias de crescente complexidade: 1) modelos de comunidades, que ignoram as diferenças entre populações e espécies, representando a comunidade como uma população única que apenas difere no tamanho do corpo, 2) modelos baseados em características das espécies (*traits*), que distinguem espécies ou grupos funcionais usando apenas o peso assintótico e 3) modelos multiespecíficos que incluem parâmetros específicos para cada espécie ou grupo funcional.

Com o recente desenvolvimento do MIZER, um pacote produzido em linguagem R (*sofware* de análise de dados) para a modelação de espectros de tamanho, e destinado a facilitar o acesso a metodologias de modelação de espectros de tamanho, é provável que a utilização deste tipo de modelo aumente ainda mais, como foi o caso do pacote de *software* Ecopath.

Para permitir decisões informadas com base nos resultados de modelos de espectro de tamanhos, os seus pontos fortes e fracos devem ser avaliados. No entanto, há poucos estudos que comparam os resultados de modelos de espectro de tamanho com outras metodologias mais conhecidas, como o Ecopath. Um modelo de Ecopath de um reservatório de água na Ria Formosa de Gamito & Erzini (2005) parece ideal para um estudo comparativo, devido ao tamanho pequeno e isolamento do tejo, que permitiu a recolha de dados confiáveis para avaliar as duas abordagens.

Além disso, os modelos de espectro de tamanhos foram desenvolvidos principalmente para ecossistemas pelágicos impulsionados pelo plâncton, com componentes detríticos mínimos. Deste modo, a utilização dessa metodologia num ecossistema costeiro de reduzida

profundidade com fluxo detrítico elevado, permitirá a avaliação da adequação das metodologias de espectro de tamanho para esses ecossistemas.

Um modelo de espectro de tamanho para várias espécies dum reservatório de água da Ria Formosa foi construído usando os dados e as estimativas de biomassa de Gamito & Erzini (2005). Beta (ratio de preferência de comprimentos predador / presa) e sigma (a largura do núcleo (*kernel*) de seletividade predador-presa) foram estimados usando as proporções publicadas de área da boca e comprimento do corpo. O coeficiente de metabolismo padrão (Ks) foi estimado usando dados de consumo de oxigênio em repouso obtidos na base de dados online FishBase (2019), assumindo uma temperatura média de 19ºC. Os demais parâmetros foram obtidos também através do FishBase ou estimados usando os métodos padrão apresentados em (Scott et al., 2013). O modelo foi calibrado para o conjunto de dados de Gamito & Erzini (2005); o conjunto de parâmetros levou a um estado estacionário. No entanto, a estimativa de parâmetros mostrou-se difícil, o que aumentou a incerteza baseada nos parâmetros.

Durante a estimativa inicial de Q/B, algumas estimativas extremamente irreais foram obtidas. Estas foram atribuídas à inclusão de muitas espécies de baixa abundância e biomassa, uma vez que estas espécies tinham valores estimados de Q/B muito elevados. Além disso, estudos anteriores alertam para o facto de o MIZER poder apresentar dificuldades no caso de um elevado número de espécies de baixa abundância e biomassa, o que também acontece com o Ecopath.

As estimativas de consumo / biomassa (Q/B), produção / biomassa (P/B), mortalidade devido a predação, composição da dieta e parâmetros de crescimento para cada modelo foram obtidas e comparadas. Como o modelo de espectro de tamanho usou um formato multiespecífico para a maioria das espécies, enquanto o modelo de Gamito & Erzini (2005) apenas modelou explicitamente duas espécies, as estimativas específicas para cada espécie do modelo de espectro de tamanhos foram agrupadas nos mesmos grupos funcionais de Gamito e Erzini (2005), usando médias ponderadas.

No modelo MIZER, as taxas de crescimento de diversas? espécies parecem reduzidas pela diminuição da disponibilidade de alimento. O modelo previu, do mesmo modo, valores de W∞ (peso assintótico) inferiores aos estimados a partir dos dados ou do FishBase, com baixos níveis de alimentação em tamanhos maiores oferecendo uma possível explicação. Pensa-se que o declínio na taxa de alimentação com aumento de tamanho foi agravado pela concentração da maioria da biomassa nas classes de tamanho mais pequenas, causando uma baixa disponibilidade de itens de presas maiores. O Ecopath previu valores inferiores de W_∞.

Em geral, o modelo Ecopath previu valores mais elevados de Q/B, P/B e de mortalidade por predação, sendo a diferença substancialmente superior para os grupos funcionais dos invertebrados. As mortalidades de predação mais elevadas e estimativas de Q/B e P/B foram atribuídas ao núcleo (*kernel*) da seletividade predador/presa tornando parte das espécies de presas inacessíveis aos predadores, devido à inexistência ou reduzido número de predadores que selecionam determinadas classes de tamanho. Como o Ecopath não inclui tamanho na determinação de presas, este modelo considera toda a população de presas igualmente vulneráveis, resultando numa maior disponibilidade de alimentos. Este aspeto poderia explicar as mortalidades de predação mais baixas previstas no modelo de espectro de tamanhos, que por sua vez causariam taxas Q/B mais baixas e, como a produção é dependente do consumo, estimativas de P/B mais baixas.

A composição da dieta prevista revelou-se semelhante à de Gamito et al. (2003), baseada na análise de conteúdos estomacais para o mesmo local de estudo. No entanto, o modelo de espectro de tamanhos previu maior consumo de plâncton, provavelmente? devido à matriz de dietas de Gamito e Erzini (2005) não incluir plâncton para muitas espécies. Este facto sugere que os parâmetros de alimentação selecionados previam com precisão as dietas dessas espécies, potencialmente devido ao sistema de estudo ser de baixa estabilidade e diversidade, em que dietas generalistas são consideradas vantajosas. Assim, o pressuposto que os animais alimentam-se de todas as presas que se encontram na sua faixa de seleção de tamanho pode representar com precisão as interações predador-presa em sistemas como esse do tipo da Ria Formosa.

Este estudo produziu um modelo de espectro de tamanho de várias espécies de um reservatório de água da Ria Formosa e comparou-o com um modelo de balanço de massa estática do mesmo sistema usando o mesmo conjunto de dados na plataforma Ecopath. As estimativas de Q/B, P/B, mortalidade por predação e composição da dieta dos dois modelos foram comparadas. As estimativas Q/B, P/B e mortalidade por predação do Ecopath foram geralmente mais altas do que as do modelo de espectro de tamanho, possivelmente porque os parâmetros de alimentação beta e sigma limitavam a disponibilidade de presas. As composições das dietas foram semelhantes entre os modelos, além do espectro de tamanhos prever uma maior proporção de plâncton nas dietas de quase todas as espécies. A estimação de parâmetros mostrou-se difícil,

com os métodos padrão evidenciando-se inadequados. Os resultados destacam a necessidade de metodologias aprimoradas para a estimação de parâmetros, de forma a permitir maior captação de alimento, e minimizar a incerteza baseada em parâmetros dessas metodologias.

Abstract

Size-spectrum modelling methodologies have been gaining popularity, with the recent development of MIZER, a size-spectrum modelling package intended to provide scientists access to size-spectrum modelling methodologies, uptake of these will likely increase.

Few studies comparing size-spectrum models to other methodologies have been performed. An Ecopath model of a water reservoir in the Ria Formosa by Gamito & Erzini (2005) presented an ideal comparison model. A multi-species size-spectrum model of this ecosystem was constructed and calibrated using the data from Gamito & Erzini (2005); parameters were estimated from FishBase or published data. These parameters led to steady state.

Consumption/Biomass (Q/B), Production/Biomass (P/B), predation mortality, diet composition and growth parameters for both models were estimated and compared. The Ecopath model predicted generally higher predation mortality, Q/B and P/B, with this difference being much greater for invertebrate functional groups. This was attributed to feeding parameters beta & sigma limiting prey availability compared with the Ecopath model; production is consumption dependent, therefore lower predation mortalities and Q/B would result in lower P/B estimates.

The size-spectrum model predicted higher consumption of plankton than Ecopath, due to the Gamito & Erzini (2005) diet matrix not including plankton for many species. Otherwise the predicted diet composition was similar to the Gamito et al., (2003) stomach content analysis study at the study ecosystem. Suggesting these feeding parameters accurately predicted the diets of these species.

The growth rates of many species in the size-spectrum model appeared stunted by decreasing food availability. MIZER also predicted W_∞ (asymptotic weight) values lower than those estimated from the data or FishBase, with low feeding levels at larger sizes offering a potential explanation. Ecopath predicted the lowest W_∞ values. Parameter estimation proved difficult with default methods being unsuitable. Therefore, many were estimated from published data, resulting in increased parameter-based uncertainty, highlighting the need for improved methodologies for parameter estimation.

Keywords; MIZER, ECOPATH, SIZE-SPECTRUM, MASS-BALANCE, FISHERIES, COMPARISON.

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Chapter 1: Introduction

The historical track record of fisheries management has been one of catastrophic failure; these failings have highlighted the need to improve on older management tools such as single species models and surplus production models. This has stimulated rapid advancement and uptake of more sophisticated methodologies, such as ecosystem level modelling approaches (Plagányi, 2007).

Marine ecosystems are complex, encompassing a range of physical, chemical and biological factors across broad spatial and temporal scales. Many different model types have been developed to capture these interactions (Plagányi, 2007). These mostly fall into two general categories of size-based models and food-web based mass-balance models (Jacobsen et al., 2015).

However, comparisons of the outputs from these are distinctly lacking (Blanchard et al., 2017); with only a handful of studies attempting this (Jacobsen et al., 2015; Spence, et al., 2018). This thesis aims to give an objective comparison between a size-spectrum and a food-web mass-balance model, whilst also highlighting issues regarding the parameterisation and use of these.

This chapter gives a brief review of the principles behind these model types, new developments, applications and the need for comparative studies.

Size-spectrum models

Key concepts

Size plays an important role in the structuring of marine communities; influencing growth, mortality, reproduction (Woodward et al., 2005), movement (Ware, 1978) and predation (Cohen et al., 1993; Scharf et al., 2000). Furthermore, many marine species, undergo dramatic changes in size, body morphology and trophic level during their lifespans (Jennings et al., 2001).

The use of these principles for modelling are based on the observations of Sheldon (1972), that when marine organisms of a particular ecosystem are sorted into logarithmic size interval bins, the total biomass of these bins remains approximately constant, known as the Sheldon-Biomass-Spectrum (fig 1.1).

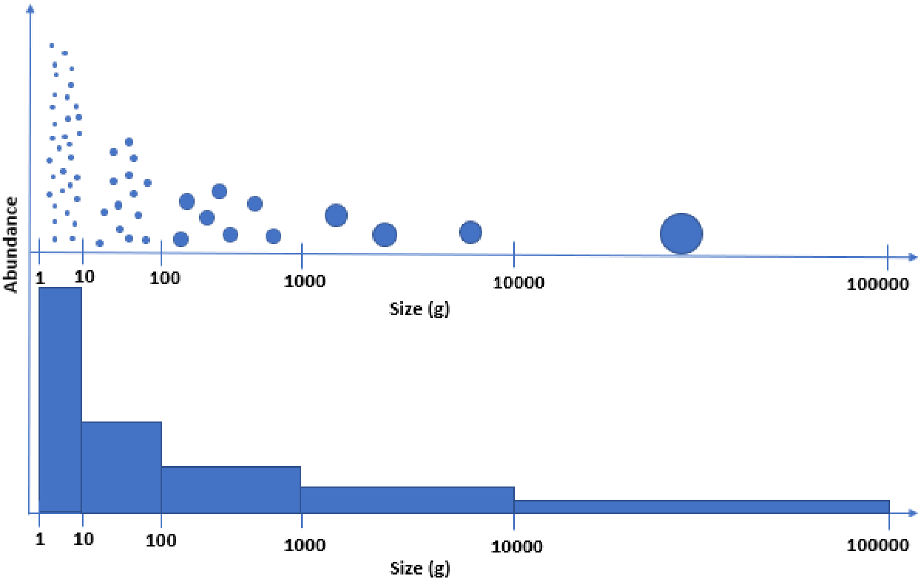

Figure 1.1. A visual representation of the Sheldon-Biomass-Spectrum (Sheldon, 1972). Organisms are represented as partials of varying sizes, when these are sorted into logarithmic size interval bins, the biomass of each bin remains approximately constant, despite the reductions in abundance.

This concept led to the definition of the ‘Biomass-Size-spectrum’ by (Kerr & Dickie, 2001): as the biomass distribution (B), or energy (E), or abundance (N), expressed as a function of an individuals size (either length, weight or volume) in a Log-Log space (Guiet et al., 2016a). There are many variations of this concept, utilising different combinations of these, with or without normalisation (Andersen et al., 2015). These principles are demonstrated by the community size-spectrum (fig 1.2); this is a simple model as it ignores differences between populations and species, representing the community as a single population who only differ in body size, species are not resolved with the slope representing the community average (Blanchard et al., 2009).

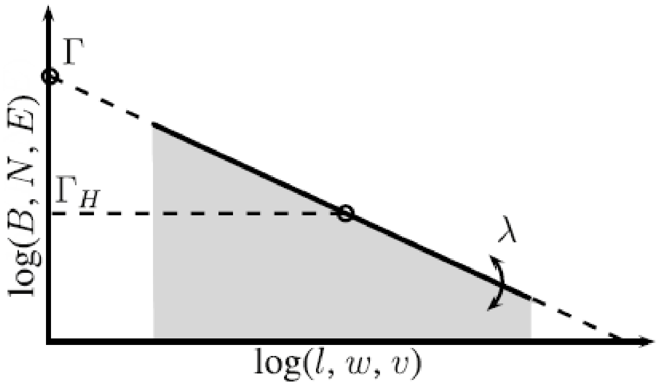

Figure 1.2. The linear community size-spectrum: λ *represents the slope of the* Γ *spectrum, the intercept* Γ *and* Γ_H *is the mid-point height. (adapted from Guiet et al., (2016a).*

The intercept (fig 1.2) indicates the richness of an ecosystem, with productive eutrophic ecosystems showing higher intercept values than oligotrophic ecosystems with low productivity. The intercept can be considered an in indicator of environment influence, whilst also linking the primary productivity of the ecosystem with the size-spectrum (Boudreau & Dickie, 1992).

The slope is dependent upon the values of biomass distribution, energy and abundance. The smooth linear slope shown in fig 1.2 represents a constant feature of unexploited steady state ecosystems (Guiet et al., 2016a). Therefore, perturbations to the ecosystem will be reflected in the size-spectrum slope as a deviation from this linear slope. This has been suggested as reliable measure for assessing the impacts of fishing (Bianchi et al., 2000; Shin et al., 2005) and environmental changes (Guiet et al., 2016b), due to changes in the sustained length of the trophic chain.

Biomass transfer is predation driven and based upon the concept that big fish prey upon small fish (Giacomini et al., 2016). In community level size-spectrum models these principles link the biomass size-distribution with predation-driven biomass transfer from smaller prey to larger predators (fig 1.3). At an individual level biomass [$P(S_i,S_j$] consumed by the predator (S_i) is converted in predator mass by growth; growth is limited by the metabolic costs of the predator and the assimilation efficiency of predated biomass (fig 1.3) (Maury et al., 2007; Guiet et al., 2016a). Mesopredators (S_i) are themselves prey for larger apex predators resulting in a transfer of energy/biomass to larger size-classes, this results in the community level biomass distribution, summing the biomass of all individuals in increasing size classes (Maury et al., 2007; Guiet et al., 2016a) (fig 1.3).

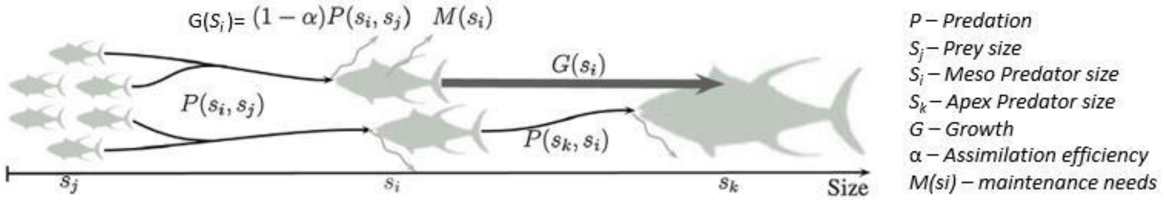

Figure 1.3 Individual level biomass transfer from smaller prey to larger predators. Predation fuels growth, which is limited by the assimilation efficiency and maintenance needs of the predator. Adapted from Guiet et al., (2016a).

These individual level processes (fig 1.3) integrated at the community level result in an abundance flux from size S to S+Δ controlled by growth and size-selective predation (fig 1.5); the size-selectivity of predation is controlled by the predator/prey size ratio ($S_{i,j}$), which controls what portion of the size-spectrum is available as prey.

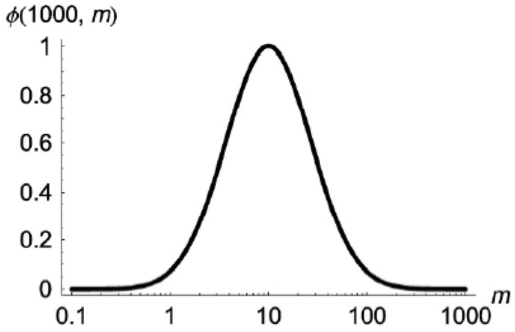

Figure 1.4. the size selection of prey for a theoretical predator with a mass of 1000g; the predator/prey mass ratio ($p(s_i: s_j)$) of 1:10. adapted ftom Andersen & Beyer, (2006).

to the predator (fig 1.4). Individual growth is represented by *g*, mortality by *S*, which is controlled by predation, availability of food in the form of smaller individuals, a background resource (normally plankton). The flux of individuals with time is determined by reproduction of mature individuals within the size-spectrum (population). The processes involved in the predation driven growth on an individual can be seen in figures 1.5 and 1.6.

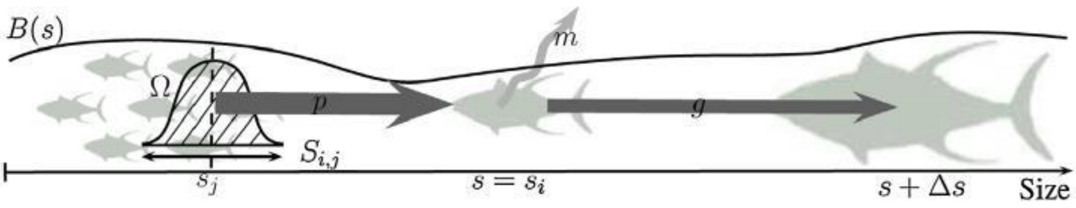

Figure 1.5. Processes in the community level biomass transfer. Adapted from Guiet et al, (2016a).

This represents a fundamental concept in size-spectrum modelling: growth and reproduction are fuelled by predation, which also provides the maintenance energy for the organism. This is controlled by the McKendrik Von-Foerster equation (equation 1.1) which combines a growth and sink term to account for predation and other mortality (e.g. fishing).

Equation 1.6. The McKendrik von-Foerster equation (M'Kendrick, 1925; Von-Foerster, 1959).

$$\frac{\partial N_i(w)}{\partial t} + \frac{\partial g_i(w)N_i(w)}{\partial w} = -\mu_i(w)N_i(w)$$

$\partial N_i(w)$ = density of individuals
$g_i(w)$ = individual growth
$\mu_i(w)$ = individual mortality
(w) = weight

The McKendrik-von Foerster equation (equation 1.1): is relatively simple conservation equation, representing the processes of biomass transfer from the small to large size-classes of the size-spectrum mediated by predation and growth (fig 1.6). This concept of food-dependent growth is fundamental to size-spectrum modelling (Andersen et al., 2015).

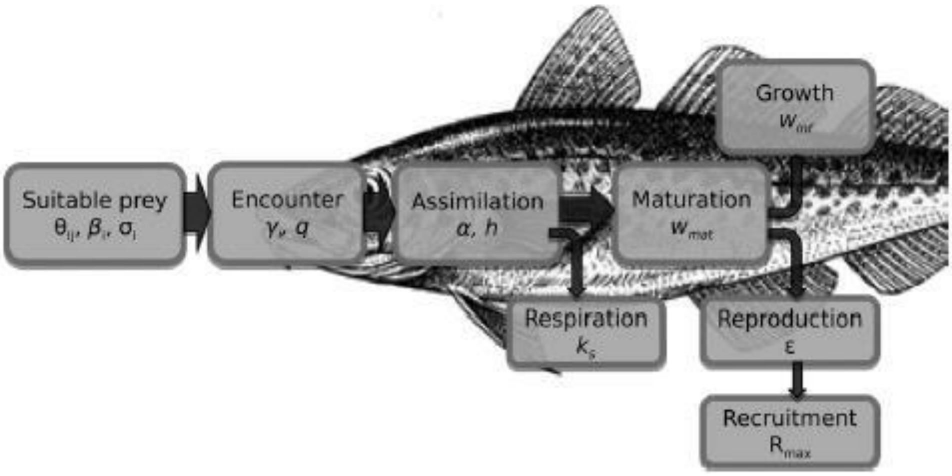

Figure 1.61. The energy pathways involved in predation fuelled growth according to the McKendrik-von Foerster equation Adapted from Scott, Blanchard, & Andersen, (2014).

Multiple functions have been added to this including reproduction as a boundary condition, as well as various types of mortality including ageing, disease, starvation and fishing mortality (Guiet et al., 2016a) (fig 1.7).

To avoid biomass accumulation at the highest-size classes due to low mortality as predation and natural mortality decline with size, it must be 'closed' at the highest size classes. This can be done by additional senescence mortality or predation by a theoretical super predator (Guiet et al., 2016a).

In order to provide the smallest individuals with food, a resource size-spectrum is included (Equation 1.2). This is normally used to model plankton and begins at a much smaller size than the fish size-spectrum, as this is necessary to provide food for the smallest individuals in this.

Equation 1.2. Semi-chemostat equation describing the background resource spectrum (Scott et al., 2013).

$$\frac{\partial N_R(w,t)}{\partial t} = r_p(w)\Big[c_p(w) - N_R(w,t)\Big] - \mu_p(w)N_R(w,t).$$

$N_R(w).$ = *the resource spectrum*

$r_p(w)$ = *Plankton regeneration rate*

$c_p(w)$ = *The carrying capacity in the absence of predation*

t = *Time*

With allometric scaling as: $r_p(w) = r_p\, w^{n-1}.$ $c_p(w) = \kappa\, w^{-\lambda}.$

(λ) = to the exponent of the background spectrum

Size-spectrum models: Incorporation of ecological processes

Marine ecosystems are highly complex and dynamic; in order for the model to produce an output which is representative of that particular ecosystem, these must be incorporated into the size-spectrum (fig 1.7).

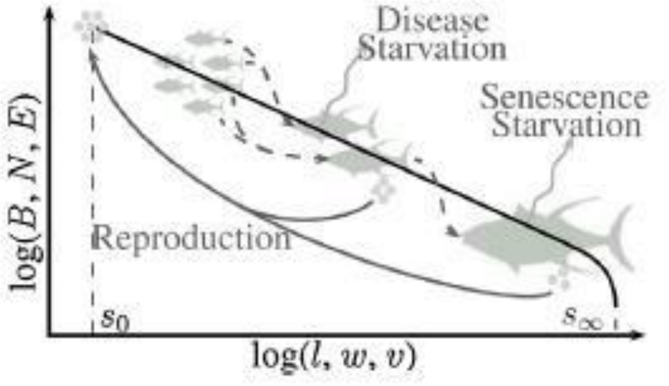

Figure 1.7. Inclusion of additional ecological processes in the community size-spectrum, black arrows represent biomass fluxes and grey arrows represent biomass loss Adapted from Guiet et al., (2016a).

Predator-prey encounters fuel individual growth (Equation 1.1), these will also vary between systems and with the size and species of the predator. The prey available to the predator is specified by integrating all individuals and background resources into the prey size selection (fig 1.4; Equation 1.3), with the encountered prey depending upon the predators search rate, which increases with the predators weight, due to the lower frequency of larger prey items (Andersen & Beyer, 2006) (fig 1.1).

Equation 1.3. Predator prey encounter rate (Scott, Blanchard, & Andersen, 2013).

$$E_i(w) = \gamma_i(w) \int \left(\sum_j \theta_{ij} N_j(w_j\, w\, (\; \theta_{ip} N_R(w_p) + \right) \phi_i(w, w_p) w_p \, dw_p.$$

i = Predator species
w = Weight
w_p. = Prey weight
$\gamma_i(w)$ = Overall predation prefactor (can be interpreted as search volume)
$\gamma_i(w) = \gamma_i w^q$. = Default allometric scaling of the predation prefactor

In reality it is not possible for all the encountered food to be consumed, at a certain point the predator will become satiated (unable to consume more). This is represented by the feeding level, a dimensionless number determined by a Holling type two functional response (Holling, 1959), with a range from 0, no food, to 1, full satiated (equation 1.4). Therefore, the proportion of encountered food consumed is the 1 – the feeding level.

Equation 1.4. Estimation of feeding level (proportion of encountered food consumed) with allometric scaling (*Scott et al., 2013*).

$$f_i(w) = \frac{E_i(w)}{E_{e,i}(w) + h_i(w)}, \quad \text{With allometric scaling as:} \quad (1 - f_i(w))E_i(w) = f_i(w)\,h_i(w).$$

$f_i(w)$. = Feeding level

$h_i(w)$ = Maximum consumption rate

$1 - f_i(w)$ = Proportion of food actually consumed

Reproduction is also a significant process not only for the continuation of populations and species, but in relation to the size-spectrum it takes biomass from the larger size-classes and transfers to the small size-classes in the form of eggs and juveniles (Scott et al., 2013). To integrate this process (Maury et al., 2007), assumed that egg production corresponds to the fraction *1-k,* with *k* being defined as the fraction of the assimilation energy allocated to the growth and somatic maintenance (Fig 1.8), which is diminished by a maintenance cost of *(1-k)/k,* multiplied by the body weight (Kooijman, 2000; Miller, 1985).

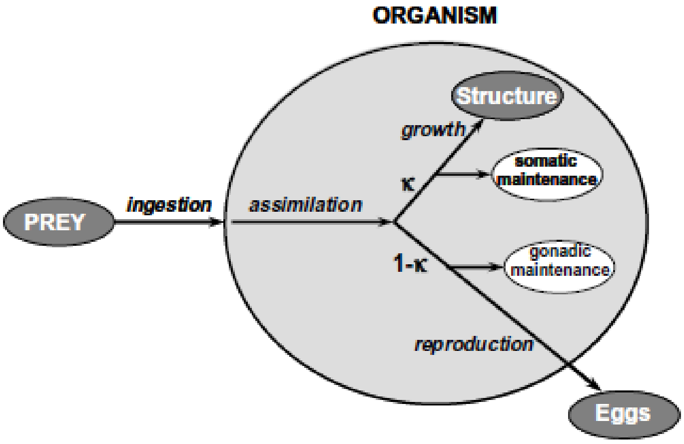

Figure 1.8. Visual representation of the energy allocation in an organism Adapted from Maury, et al., (2007).

Reproduction is modelled as a resource dependent process, which can simulate starvation when insufficient prey is available. This was modelled by Maury et al. (2007) as a net dissipation of mass in the size-spectrum; growth and reproduction cease as these are resource dependent, and the deficit between mass consumption and maintained requirements is removed from the size-spectrum.

Size-spectrum models were originally developed in order to model pelagic phytoplankton-driven ecosystems with minimal detrital components; in these systems fish are the primary component, with size-selectivity strongly influencing predatory interactions (Blanchard et al., 2017). However, shelf seas with large detrital components are challenging to model using the size-spectrum approach, due to species exhibiting non-size selective feeding on detritus, which can support large biomasses of microbenthic organisms (Greenstreet, 1997).

It is however possible to include these pathways in the size-spectrum. Blanchard et al. (2009) used data of the entire community for the North Sea (both benthic and pelagic components), which had been sorted into $\log^2$ body mass bins, and the species classed as either ‘benthic detritivores’ (benthic invertebrates) or ‘pelagic predators’ (fish and epifaunal invertebrates), the search rate of the detritivores was assumed to be 10% that of the pelagic predators due to their sedentary nature. These data sets were then used to produce community size-spectrum slopes for both components (fig 1.9); detritus was included as a non-size-structured food pool available to the detritivores, the two slopes were linked with predatory interactions and detritus production from the predator slope being transferred to the detritus food-pool.

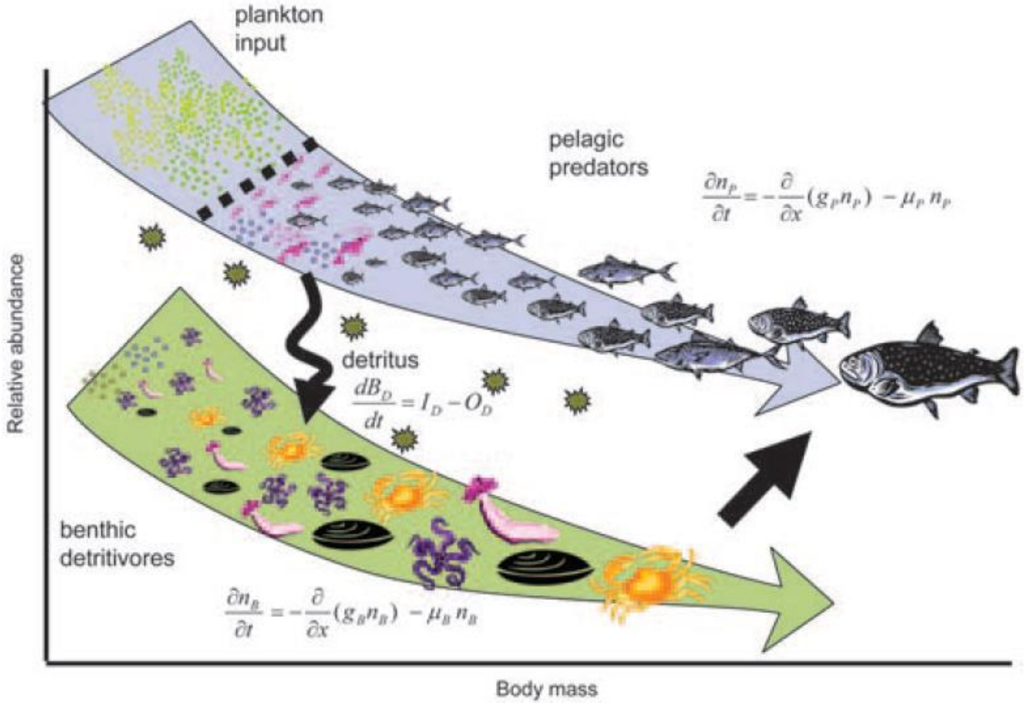

Figure 1.9. Conceptual illustration of the ‘benthic detritivore’ and ‘pelagic predator’ community size-spectrum slopes. The pelagic predator community represents predators feeding upon increasingly larger prey as they grow. The benthic detritivore slope represents benthic organisms competing for the same food source, detritus. The two slopes are linked by predatory interactions, and detritus produced by the pelagic predator spectrum is injected into the benthic detritivore spectrum adapted from Blanchard et al., (2009).

This represents a significant advancement in the progression of size-spectrum models making them applicable to a wider range of ecosystems.

Size-spectrum modelling: recent developments

The section above is referring to community size-spectrum models; these can be considered as the simplest version of size-spectrum models with size being the only structuring factor in the spectrum (Guiet et al., 2016a). Therefore, disregarding species-specific differences between individuals of the same size such as physiological and metabolic differences, growth rates and maturation size (Guiet et al., 2016a). This will clearly give a lower resolution of the ecosystem, as non-predatory interactions can have a significant influence on population dynamics.

One approach to include these parameters in the model workings is the trait-based-model by Andersen & Beyer (2006), which resolves a group of species by their 'traits' of which asymptotic weight W_∞ (a parameter of the von-Bertalanffy growth curve, representing the mean length of a species of a given stock would reach assuming an infinite growth period FishBase, (2018)) is considered the most important, regarding the species life history. For example, Andersen & Beyer (2006) found species with lower asymptotic sizes to have higher abundances, metabolisms, growth rates and food demands than species with larger W_∞.

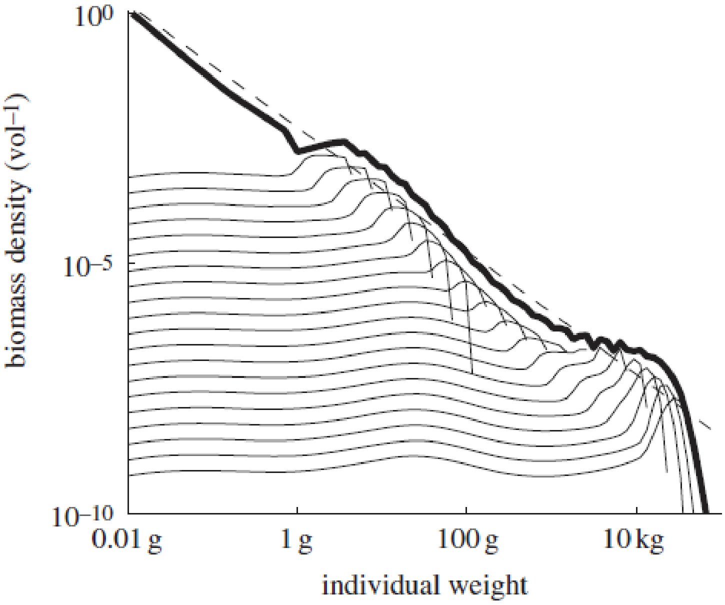

Figure 1.10. an example of a size-spectrum derived from a trait-based model. The thick line represents the community size-spectrum with the thin lines representing the size-spectrum of each trait class, the dashed line is the theoretical community size-spectrum (Andersen & Pedersen, 2010).

In the trait-based model the community is represented by a discrete number of species distributed across this range of asymptotic sizes, however the number of species does not influence the model. The outputs for this give both a community size-spectrum with no differentiation based on traits (asymptotic size) and series of size-spectrum for each trait-class (fig 1.10).

This approach is more powerful and resolved when investigating ecosystems subject to multi-species fisheries, as due to economic drivers fishers often preferentially exploit species with larger W_∞, causing higher mortalities of these (Blanchard et al., 2017). This methodology has been used by several authors to investigate the community-wide impacts of selective fishing pressures, without the need for extensive, assumption filled species-specific data (Andersen & Pedersen, 2010) which can be considered major limiting factor for many modelling methodologies (Plagányi, 2007). This provides a useful tool for management of fishing pressure in relation to the entire community, when species specific trait data is unavailable (Andersen & Rice, 2010).

However, trait-based models still disregard the role of taxonomic diversity regarding life history or behaviour (Guiet et al., 2016a). While these offer a strong measure to assess ecosystem health and impacts with reduced data requirements, they lack the ability to represent biodiversity in an ecosystem (Blanchard et al., 2014). This offers a clear shortcoming when compared to other ecosystem level models such as Ecopath, which can explicitly model individual species and their interactions (Christensen & Walters, 2004a).

This led to the development of a multi-species extension of the trait-based model (Blanchard et al., 2014), which includes species specific parameters as well as W_∞ (Blanchard et al., 2017). However, appropriate parameterisation of these requires extensive species-specific data (Spence et al., 2015), similar to other species-resolved models.

The community model offers a useful tool for assessing large-scale community level questions only requiring the average spectrum (Scott et al, 2013), with the trait-based model utilising the W_∞ being a powerful tool capable of resolving complex food webs (Andersen & Pedersen, 2010). An appropriate size-spectrum approach can be utilised depending on the extent of the data set (Guiet et al., 2016a).

The development of trait-based and multi-species size-spectrum models represents a major advance in size-spectrum modelling, allowing for more detailed insight into the functioning of ecosystems. Furthermore, these overlap the previously clear differences between size-spectrum and species-resolved food-web models such as Ecopath (Blanchard et al., 2017). As objective comparisons between size-spectrum models and species-resolved food web models had previously not been possible due to fundamental model differences and lack of species specificity, this allows an opportunity to further quantify the outputs of these (Jacobsen et al, 2015). Allowing for more informed ecosystem management decisions.

Parameter estimation

The multi-species methodology greatly increases the parametrization and data requirements due to the need for species specific parameters (Blanchard et al., 2017). Many of the parameters have already been briefly covered in the previous section, with simple methodologies for estimation of these (Scott et al., 2014).

As this study employs a multi-species size-spectrum modelling framework, estimation of many species-specific and general parameters was required. The specific parameter values estimated and the methodologies for obtaining these are discussed in detail in the methods, results and discussion sections, whereas this sub-chapter aims to give a brief background on the parameters necessary for size-spectrum modelling.

As can be seen in Table 1.1, there are a wide variety of parameters necessary for the proper functioning of a size-spectrum model; several cases, as size-spectrum modelling is still in its infancy, established methodologies for estimating many of these are lacking, for example beta and sigma.

Table 1.1. Individual level, general and plankton input parameters for the construction of a multi-species size-spectrum model; units and the default value or method of calculation are provided when available. This table was compiled from Hartvig et al., (2011); Scott et al., (2013); sizespectrum.org, (2019).

Parameter	**Description**	**Default value, or method of estimation**	**Units**
Individual level parameters			
W_∞	The asymptotic weight of a species or functional group.	No default, estimates available from Fishbase, (2019).	G
Wmat	The weight when an individual of that particular species reaches maturity (FishBase, 2019).	No default, estimates available from Fishbase, (2019).	g
Beta	Preferential ratio of predator mass to prey mass.	No Default, no-default method of estimation. When no data is available 100 can be used as default.	N/A
Sigma	Width of the prey-size preference kernel	No Default, or default method of estimation. When data is not available 1.3 can be used as default.	N/A
H	Maximum food intake rate .	Default calculation using the K(vb) column.	g^{1-n}/yr
gamma	Constant for the volumetric search rate.	If this is not provided, it is calculated using the h column and other parameters.	g^{q-}m3/yr
Q	Exponent for volumetric search rate.	0.8	N/A
Ks	Standard metabolism coefficient.	h * 0.2	
K	Activity coefficient.	0	
P	Exponent of standard metabolism.	0.75	
Alpha	Assimilation efficiency, the proportion of energy diverted into growth and reproduction once the metabolic needs of the individual have been met.	0.6	
Reproductive efficiency (N)	The proportion of available energy converted into either growth or reproduction.	1	
General parameters			
Wmin	The size class that new recruits are placed in, i.e. the smallest size class of the species size Spectrum.	Calculated automatically by MIZER	*g*
Wmax	The largest size class in the size-spectrum	Calculated automatically by MIZER	*g*
No_W	Number of size-bins in the size-spectrum	Calculated automatically by MIZER	
Plankton resource spectrum parameters			
NO_W_PP	Number of size bins in the plankton size-spectrum.	round(no w) * 0.3	
Min_W_PP	The smallest size of the background size spectrum.	1e-10	*g*
R_pp	The growth rate of the primary productivity (the background spectrum).	10	
Kappa	The carrying capacity of the background spectrum.	1e11	
Lambda (λ)	The exponent of the background spectrum.	2+q-n	
W_PP_cutoff	The cut off point for the size of the plankton spectrum.	10	*g*
f0 (feeding level)	Proportion of actual food actually consumed. Can be used to estimate h and gamma when data is not available.	0.6	

Furthermore, this issue is compounded by parameter-based uncertainty being regarded as a major source of uncertainty in the outputs of size-spectrum models (Spence et al., 2015; Thorpe et al., 2015). This was investigated by Spence et al, (2015) assessing the impacts of uncertainty in input fishing parameters on the outputs of the Blanchard et al., (2014) multi-species size-spectrum model of the North Sea, finding that these had significant influences on the model outputs. Furthermore, Thorpe et al., (2015) also investigated the impacts of parameter-based uncertainty in a size-based North Sea ecosystem model, finding that after Asymptotic length (L_∞), the diet matrix and predation size-selectivity exerted the greatest influence on the models output. As accurate estimates of these are difficult to obtain, it is probable that a high uncertainty is often associated with these, highlighting the need for established methodologies for estimating these and access to existing estimates of these.

As these include parameters that are not easily obtained, this study will estimate these from existing data sets, this provides an opportunity to assess new methods of estimating these. One such set of parameters are beta, sigma and the interaction matrix, which determine the predicted diet compositions of the species present in the size-spectrum model (Scott et al., 2013). A study by Gamito et al., (2003) conducted stomach content analysis to determine the diets of the species present in the study area, this presents an excellent opportunity to compare the diets predicted by the size-spectrum model compared to those estimated from the study area.

The MIZER software package

The development of size-spectrum methodologies discussed in the previous section led to the recent development of MIZER, a software package for size-spectrum modelling in R (R Development Core Team, 2014). This software is intended to allow scientists easy access to size-spectrum modelling to investigate aquatic communities (Scott et al., 2013); MIZER is freely available and was designed to be user friendly, whilst incorporating a range of size-spectrum functions. It is possible to run community, trait-based and multi-species size-spectrum models in this program (Scott et al., 2013).

The multi-species function allows the user to resolve an unlimited number of species, each having its own set of growth, life history, reproduction and feeding parameters. Reproduction and recruitment are food-dependent. Users are able to specifiy a range of recruitment functions, however the default is the Beverton-Holt type 2 function (Scott et al., 2014); where where the recruitment flux approaches a maximum with increasing egg production (Beverton & Holt, 2012). This program is not intended for community assement but more for simulating the potential consequences of fishing for the community (Scott et al., 2013).

The development of MIZER represents a significant advancement in size-spectrum modelling, by allowing widespread use by fisheries scientists and ecologists. It is likely that this may facilitate a rapid increase in the publications using size-spectrum approaches (Giacomini et al., 2016), similar to Ecopath (Christensen & Walters, 2004b).

Ecopath with Ecosim

Introduction

Ecopath is a static mass-balance trophic food-web model originally conceived by Polovina, (1984); this was further developed in the 1990s resulting in the modelling platform Ecopath (Christensen & Pauly, 1992) with Ecosim in 1995 (Walters et al, 1997) and Ecospace in 1999 (Walters et al., 1999), collectivly known as EwE. The Ecopath package consists of three separate computational units: the original concept, Ecopath, which is a static mass-balance energy-accounting model, intended to capture trophic components, the interactions of these and their utilisation within the food web. The Ecopath formulation can be applied across temporal scales using Ecosim and across spatial and temporal dimensions with Ecospace (Christensen & Walters, 2004a).

This is a widely used approach to investigate human impacts on ecosystems (Plagányi & Butterworth, 2004). Due to its versatility, reliability and ease of use the EwE modelling approach was recognised by the National Oceanic and Atmospheric Administration as one of the top 10 biggest scientific breakthroughs of the organisations 200-year history (Christensen, 2013). The EwE program is no longer directly funded by a single institute and since 2012 has been run by the Ecopath Research and Development Consortium, which is a cooperative network of scientists focused on the research development and sustainability of the EwE. It is non-profit and subsequently freely distribute the core software and source code (Ecopath, 2019).

Ecopath with Ecosim: key concepts

The Ecopath model is based upon the principles of Polovina, (1984) who adopted the principle of mass-balance from the Laevastu model to construct an ecological accounting system. The mass-balance principle is that energy input must balance with energy output for each functional group or species that is modelled (Christensen, 2013). This is modelled by equation 1.5:

Equation 1.5. Fundamental Ecopath mass-balance equation from Polovina, (1984); Scott et al., (2013) adapted from Plagányi, (2007).

$$B_i \cdot (P/B)_i \cdot EE_i = \sum_j (Q/B)_j \cdot DC_{ij} \cdot B_j + C_i + BA_i + NM_i$$

$(P/B)i$ = production/biomass ratio for *i*.
EEi = fraction of production of *i* that is consumed within, or caught from the system(converted to detritus).
Ci = fishing mortality (landings + discards) on *i*.
$(Q/B)j$ = total food consumption per unit biomass of *j*.
$DCij$ = fractional contribution by mass of *i* to the diet of *j*.
BAi = biomass accumulation term that describes a change in biomass over the ECOPATH base-reference-unit time step.
NMi = is the net biomass migration for *i*.

If the mass can be balanced for one species, it can be done for the entire ecosystem (fig 1.11). This requires data on the predators food requirements which is compared with prey production, which must balance, meaning the predators cannot consume more prey than is produced. This adds constraints to the model, to prevent unrealistic predictions (Christensen, 2013).

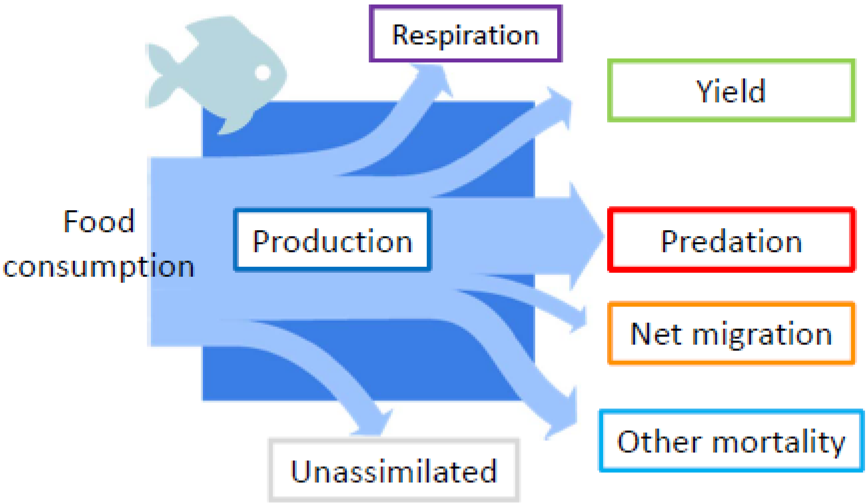

Figure 1.11. Visual representation of the mass-balance pathways used in the fundamental Ecopath mass-balance equation by Polovina, (1984).

Mass-balance can be achieved by trial and error adjustment or by utilising inverse models to minimise imbalances between inputs and outputs (Christensen & Walters, 2004a). This gives a static balanced, but not steady-state, showing the biomass fluxes, which gives a representation of the ecosystem, interactions within this and any exploitation. An example Ecopath output is given in figure 1.12.

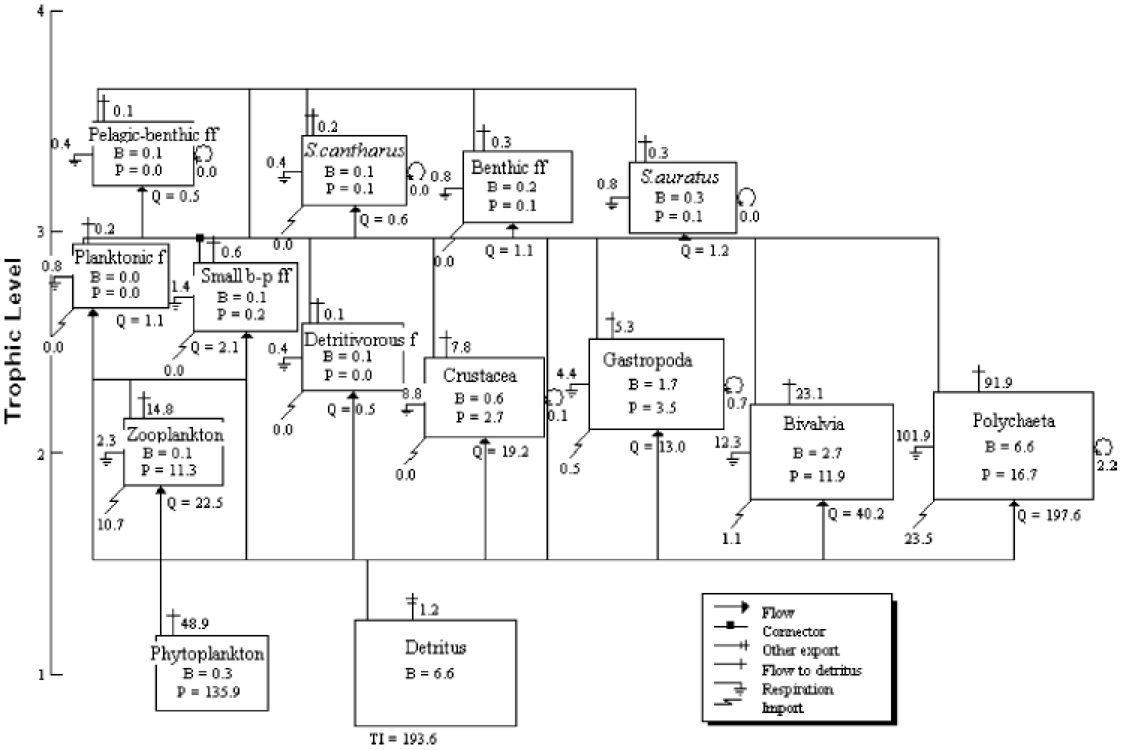

Figure 1.12. A flow chart of the trophic mass flows from the Ecopath model of a water reservoir in the Ria Formosa (adapted from Gamito & Erzini, 2005).

Ecosim works by converting the Ecopath model from steady-state trophic pathways into time dependent predictions (Walters et al, 1997). This is a valuable tool for investigating the long-term impacts of anthropogenic pressures such as fishing and climate change (Christensen, 2013).

An issue during the development of Ecosim were predator-prey interactions, as these were originally built around Lotka-Volterra dynamics. This means the consumption of predators was estimated by the number of predators multiplied by the number of prey, multiplied by the search rate, so as predators and prey increase so does consumption. There were issues with this methodology as these were essentially based upon the thermodynamic mass-action principle, however biological communities are obviously far different to randomly moving particles (Christensen, 2013). Using these predator-prey dynamics models were unstable and often experienced self-simplification, meaning it was impossible to maintain ecologically similar groups with top down control, as the poorer competitor became extinct (Christensen, 2013).

This led to addition of behaviour to predator-prey modelling; this was done using the foraging arena theory by Ahrens et al., (2012), where organisms occupy one of two states, available or unavailable for predation, achieved by adding another parameter, a behavioural exchange coefficient, to the Lotka-Volterra equation (Christensen, 2013). This stabilised the models, allowing replication of the population trends of the community (Christensen & Walters, 2004a).

Ecopath: new developments and limitations

Due to its popularity and the current consortium-based research and development, the workings of the platform have been well studied, with many modifications and features being added to improve model accuracy. A previous issue was poor differentiation between different life stages of the species; however more recent versions include the multi-stanza function, which can give multiple life history stanzas for each species, this allowed for more accurate representation of size or life stage dependent interactions, such as juvenile-adult cannibalism, however this has high data requirements (Plagányi, 2007).

EwE has achieved a balance between simplicity, allowing it to appeal to a range of users whilst maintaining the level of complexity necessary for ecosystem representation (Plagányi & Butterworth, 2004). With strengths including inclusion of well-balanced conceptual realism, representation of predator-prey interaction terms, structured parameterisation framework and the use of a general framework allowing for simple comparisons between models of different ecosystems (Christensen & Walters, 2004a). However, it still has short comings which due to the progression of EwE and its popularity are well studied (Plagányi & Butterworth, 2004). These include projections from an Ecopath steady-state model such as unrealistic life history responses, for instance compensatory changes in the natural mortality of marine mammals, and inaccuracies from extrapolating from the micro to macroscale (Plagányi, 2007).

Many problems associated with EwE can be attributed to operator error rather than the model structure (Plagányi, 2007). Uncritical use of default parameters, vulnerability settings, or excessive trial and error balancing, can lead to unrealistic model output (Ainsworth & Walters, 2015). Use of the default parameter or vulnerability values across all species is a good example of this, as it assumes the same pre-exploitation history for all populations and species possibly resulting in over compensation in stock recruitment relationships (Plagányi & Butterworth, 2004). However issues such as these often are a result of the quantity and reliability of the available data (Blanchard et al, 2017), which can further increase uncertainty regarding the parameters

Despite these limitations and extensive data requirements, EwE is still among the most widely used and well-studied modelling platforms. Due to the high numbers of authors critically reviewing the advantages and disadvantages of this platform and the mathematical concepts behind this are well understood (Christensen & Walters, 2004a; Plagányi & Butterworth, 2004). Therefore, Ecopath offers an ideal platform for comparison with a multi-species size-spectrum model.

Justification

Considering the predicted increase in the use of size-spectrum modelling (Giacomini et al., 2016); it is critical that as these models become more frequently used as management tools, objective comparative studies comparing the size-spectrum approach to other more well know modelling methodologies are conducted. These will aid policy makers when making informed management decisions, as model-based uncertainty complicates policy making (Plagányi, 2007). Furthermore, currently only a handful of studies comparing different modelling types and platforms have been published (Jacobsen et al., 2015; Woodworht-Jefcoats et al., 2015; Smith et al., 2015; Spence et al., 2015).

However, Smith et al. (2015) used a multi-species, but size based rather than size-spectrum, model in the software Atlantis, whereas Woodworht-Jefcoats et al. (2015) used a community size-spectrum model. Furthermore a study by Spence et al. (2018) compared the outputs of five different models of the North Sea including a size-spectrum model, however the objectives of this study were combine these using a statistical meta-model, collating prior beliefs, model estimates and direct observations, as an attempt to assess uncertainty in the predictions of these models. A study by Jacobsen et al. (2015) of the California current fish community, represents the only comparison of trait-base size-spectrum model to an existing model in EwE.

A study by Gamito & Erzini (2005) built and parameterised a static mass-balance food-web model using Ecopath of an isolated water reservoir in the Ria Formosa lagoon in Southern Portugal. Due to its small size and isolation it was possible to obtain accurate fisheries independent data of the size structure of the fish community and many environmental and species-specific parameters. The lagoon was isolated from the rest of the system using a net preventing immigration and emigration, the surface was covered with ropes to prevent fishing or predation by birds. The extent and confidence in this data set is ideal for a multi-species size-spectrum model. This offers a rare opportunity for a much-needed comparison of a multi-species size-spectrum model with a species-specific mass-balance food-web model in the well-known program Ecopath. Furthermore, as size-spectrum models are more commonly used for representation of pelagic ecosystems with weak detrital influences, it will provide an objective analysis of the suitability of size-spectrum for detritus-based ecosystems, compared with the Ecopath model. These findings will be essential for scientists and policy makers to make informed decisions based upon these models.

In addition the development of this size-spectrum model will require parameters which lack established procedures for estimation; requiring this study to estimate these from existing data sets, providing an opportunity to develop and assess new methods of estimating these.

One such set of parameters are beta, sigma and the interaction matrix, which determine the predicted diet compositions of the species present in the size-spectrum model (Scott et al., 2013). As these parameters are difficult to obtain, it is probable that many studies will have a high uncertainty attached to these, highlighting the need for established methodologies for estimating these and access to existing estimates.

As a study by Gamito et al. (2003) conducted stomach content analysis to determine the diets of the species present in the study area, this presents an excellent opportunity to compare the diets predicted by the size-spectrum model to those estimated for the study area, allowing for a measure of reliability of these predictions.

Using the data set from Gamito & Erzini (2005), this study will (i) construct a multi-species size-spectrum model of the water reservoir in the Ria Formosa lagoon using the MIZER package. (ii) Estimate species-specific parameters which are not available from Gamito & Erzini (2005) or FishBase, and (iii) assess the accuracy of these by comparing alternate estimates or data where available. (iiii) Calibrate the size-spectrum model using the date set of Gamito & Erzini (2005) and (iv) compare the predicted consumption/biomass, production/biomass, predation mortality, growth parameters and diet composition from both the size-spectrum model in MIZER and the Gamito & Erzini (2005) Ecopath model.

Chapter 2: Methods

The size-spectrum model

The size-spectrum model was constructed using the MIZER software package in R (R Development Core Team, 2014). This is a multi-species model with species-specific life-history parameters for the following fish species: *Anguilla anguilla*, *Atherina cf. boyeri*, *Belone*

belone, *Chelon labrosus*, *Dentex dentex*, *Dicentrarchus labrax*, *Dicentrarchus punctatus*, *Diplodus annularis*, *Diplodus sargus*, *Diplodus vulgaris*, *Engraulis encrasicolus*, *Halobatrachus didactylus*, *Mullus barbatus*, *Sardina pilchardus*, *Sarpa salpa*, *Solea senegalensis*, *Sparus aurata* and *Spondyliosoma cantharus*.

To represent the species which were not specifically modelled, these were grouped into several large taxonomic groups: Goby sp. Wrasse sp. Annelids, Gastropods, Bivalves and Crustaceans. These were given more general life history parameters as these were modelled as individual species, however using parameters and data from multiple species. The W_{mat} and W_{∞} values were estimated from the species present in the groups, then adjusted to increases the similarity between the predicted and actual size-structures present. The growth rates were lower with lower M values (M determines the proportion of available energy diverted into reproduction opposed to growth) than those of single species groups in order to spread the individuals more evenly across the size classes and avoid accumulation in one size class.

The size-classes used in the model ranged from 0.000475 – 15100g on a logarithmic scale (Scott et al., 2013). The models run time was kept at the default of 50 years (Scott et al., 2013), meaning that the parameters had to lead to a steady state within this time frame.

Data

This study used the same data set as the Gamito & Erzini (2005) model, who conducted the methodologies outlined in this section. The ecosystem selected by Gamito & Erzini (2005) was a water reservoir of the Aquamarim farm, in the Ria Formosa lagoon. This has an average depth of 2m, with an area of 1.0ha. Due to the high-water replenishment rate caused by the strong tidal currents within the lagoon, this was considered to have very similar abiotic factors to the rest of the Ria Formosa (Gamito et al., 2003; Gamito & Erzini, 2005).

A 0.6ha area of the reservoir was isolated for the sampling area; this was done using a net of $2cm^2$ mesh fixed across the benthos preventing immigration and emigration of large fish. The water's surface was covered with ropes to prevent bird predation and fishing.

The abiotic and biotic parameters were analysed from May 1996 to October 1997, with all sampling being conducted in the morning from 9:30 – 12:30. Water samples were collected twice per month during neap and spring tides. Temperature, dissolved oxygen, salinity and biochemical oxygen demand (BODs) were determined. However, only data on fauna from September 1996 to August 1997 were considered.

Macro-benthos and supra-benthic communities

The macro-benthic and supra-benthic communities were sampled every month. Eight 0.01m^2 sediment cores were taken then sieved using a 0.5 mm mesh sieve. Four of these cores were collected in the middle of the reservoir and four near the borders. The fauna collected was identified to species level whenever possible and weighed. The biomass and abundance density were then calculated.

Two sledge-hauls were performed at the same locations where the sediment cores were collected, these each covered an area of approx. 5.6m^2 (each). The sledge hauls have a net mouth diameter of 0.5m and a 1mm diameter mesh, allowing for collection of fauna from 0-20cm above the sediment surface. These collected mysids, shrimps, crabs and small fish which were counted, measured and weighed.

Fish

The fish component of the reservoir was sampled mainly using a beach seine net with a 14mm mesh, however there was also some supplementary sampling with hook and line and on one occasion, gill net. All fish were identified to species level, measured to the nearest 0.5cm and most were weighed to the nearest gram, with some weights estimated using length-weight relationships from FishBase (2019).

The individual weights were summed by species and converted to dry weight by multiplying by 0.27 (Gamito, 1994), the biomass density in dry weight per m^2 was then calculated by dividing by 6000, as the study area was 6000m^2 (0.6ha). Finally, the biomass density was divided by 6, as six beach seines were performed, with the majority of individuals being released, resulting in a high likelihood of repeat captures. Samples from 1996 were not included in the biomass estimates. The abundance density for each species was calculated by summing the total individuals caught by species, then again dividing by 6000 and then 6.

Parameter estimation

Preferred predator-prey mass ratio (beta)

Beta is the preferred predator-prey mass ratio and sigma is the width of the preferred predator-prey mass ratio kernel as the preferred prey weighted by a log-normal selection model (Ursin, 1973; Scott et al., 2013).

Estimates for both beta and sigma are hard to obtain and no data on prey size preference was collected by Gamito et al.,(2003). As data on predator-prey size-selectivity was unavailable, therefore estimates were derived using the allometric relationships for the predators mouth area as a function of its length presented in (Karachle & Stergiou, 2011) for 61 Mediterranean fish species. The total length, horizontal and vertical mouth opening were measured, these were then used to estimate the mouth area, using the assumption that mouth area is an elliptical shape (equation 2.1) (Erzini et al., 1997):

Equation 2.1. Mouth area estimation (A), assuming A is an elliptical shape *(Erzini et al., 1997). HMO refers to the horizontal mouth opening and VMO refers to the vertical mouth opening,* $\prod$ *= 3.14.*

$$A = \pi(\frac{HMO}{2})(\frac{VMO}{2})$$

To establish a relationship between mouth area and total length a power regression was used (equation 2.2).

Equation 2.2. Allometric relationship of a predator mouth area as a function of total length. A = mouth area, L = total length (cm) aA = the coefficient of shape, bA = the power fulfilling the dimensional balance (Karachle & Stergiou, 2011).

$$A = a_A L^{b_A}$$

The relationships presented by Karachle & Stergiou (2011) included eleven species present in the model, however for the remaining nine the most similar species (normally most closely related) from the 61 species studied by Karachle & Stergiou (2011) were used. These substitutions are presented in Table 2.1, unfortunately no data was available for *C. labrosus* so a reasonable value was estimated based on the assumption that it feeds mainly on small plankton and detritus (FishBase, 2019).

Table 2.1. Substitute species for beta estimation.

Species	**Substitution species**
Sparus aurata	*Diplodus vulagaris*
Goby sp	*Blennius ocellaris*
Dicentrarchus punctatus	*Dicentrarchus labrax*
Solea senegalensis	*Monchirus hispidus*
Mullus barbatus	*Mullus surmuletus*
Diplodus sargus	*Diplodus vulagaris*
Wrasse sp	*Symphodus tinca*

These relationships were then used to derive the formula for beta, which was done in several steps:

First the morphometric relationship between predator length (L) and weight (w) from FishBase (2019); (a) is the intercept of the regression curve and (b) the regression coefficient:

$$w = aL^b$$

was inverted to give L as a function of W:

$$L = \left(\frac{w}{a}\right)^{1/b}$$

The assumption was then made that preferred prey size (w_p) scales with the mouth area:

$$w_p = a_p A^{b_p}$$

No data on *ap* or *bp* (equation 2.2) was available, but *bp* was eliminated by substituting the expression for A and then expressing L by w giving:

$$w_p = a_p\left(a_A\left(\frac{w}{a}\right)^{b_A/b}\right)^{b_p} = a_p\, a_A^{b_p}\, a^{-(b_A b_p)/b}\, w^{(b_A b_p)/b}$$

And if part of this is isolated:

$$(b_A b_p)/b = 1$$

Beta is the preferred prey size (w_p), as a fixed fraction of the predator size (w), expressed as:

$$w_p = w/\beta$$

Therefore, with beta as the subject:

$$\beta = w/w_p$$

And hence, these are combined for the final beta estimation equation:

$$\beta = w/w_p = \frac{a}{a_p} a_A^{b/b_A}$$

As *ap* is not known, the reasonable value of 0.1 was used.

This allowed estimation of the beta values for the fish species. However, no data on beta values for invertebrate species is available, therefore the value of 100 was used for Annelida, Crustacea and Gastropoda with 1000 being used for Bivalvia, due to them being filter feeders and likely select smaller food items.

The beta estimates for the planktivorous fish were excessively low, considering they are planktivores (FishBase, 2019). Therefore, the beta value from Spratt from Blanchard et al. (2014) was used for the planktivorous fish as this was considered to have a similar size and feeding strategy as *S. pilchardus* and *E. encrasicolus*.

The mouth area to body length relationships proved unsuitable for sigma estimations; therefore, the reasonable value of 2.0 was used. This is within the range of sigma values, 0.8-3.2, used by Blanchard et al. (2014), leading to reasonable predictions of diet, these estimates were increased slightly in some cases to allow the species access to a wider size-range of prey.

von Bertalanffy parameters

The von Bertalanffy input parameters: asymptotic weight (W_∞), maturation weight (Wmat), K(vb) (von Bertalanffy growth coefficient), and t_0 (von Bertalanffy growth parameter defined as the age when the fish has a length of 0, as this is not the case for most species, this is normally negative), were obtained from (FishBase, 2019). The temperature was assumed to be 19°C, consistent with the Gamito & Erzini (2005) model.

Other mortality

Other mortality (z_0) is mortality not caused by either fishing or predation, this was calculated using the default method from (Scott et al., 2013) using:

$$z0 = z0_{pre} W_{inf}^{z0_{exp}}$$

With the default value of 0.6 and 1/3 being used for z0pre and z0exp respectively (Scott et al., 2013) and the W_∞ estimates from FishBase (2019).

Assimilation efficiency

The default value of 0.6 was used Assimilation efficiency (α), the proportion of the energy obtained from consumption used for growth and reproduction (production of biomass) (Scott et al., 2013).

Model calibration

In order to obtain reasonably realistic representations of the Ria Formosa lagoon community, the abundance and biomass density output were fit to be as similar as possible to those from the sampled individuals. This required adjustment of a variety of parameters.

Feeding level

The feeding level is the proportion of encountered food actually consumed, defined as:

Equation 2.3. E_i = encounter rate, h_i = max intake rate, w = weight (g) and i refers to the process being on an individual level (sizespectrum.org, 2019).

$$f0 = \frac{E_i(w)}{(E_i(w) + h_i(w))}$$

The feeding level (*f0*) of small individuals feeding mainly on the background resource can be assumed to 0.6 as a default value for the majority of species (Scott et al., 2013). As estimates of *h* (maximum food intake) and gamma (the volumetric search rate) were not available, these were calculated from the feeding level and the K(vb), obtained from FishBase (2019), to give a default estimate.

The default values often predicted growth curves significantly different to those based on the von Bertalanffy parameters from FishBase (2019). Therefore, the values of *h* and gamma were adjusted until the predicted growth curve was as similar as possible to the one based on FishBase (2019). However, the curves were fit to the early stages in the growth curve, as the feeding level dropped with increasing size/age, resulting in lower growth rates. The initial feeding level was maintained at approximately 0.6, despite adjustment of *h* and gamma.

Proportion of energy diverted into reproduction

The M maturity parameter (determines the proportion of energy put into reproduction once the individual has reached maturity (Scott et al., 2013)), was adjusted to fit the predicted growth curve to that from the FishBase (2019) data. Increasing M decreases the proportion of energy the individual invests in reproduction and increases the proportion used for growth (Scott et al., 2013). Most species were given high M values, due to low growth rates.

Coefficient of standard metabolism

Data on Ks (standard metabolism coefficient), which is a constant for standard metabolism for a fish of 1g, with an allometric scaling relationship as the individual grows (Scott et al., 2013), was not available. Therefore, initially the default method of estimating this was used (Scott et al., 2013):

$$Ks = h * 0.2$$

However, this gave highly varied values, most of which were completely unrealistic. This default method was therefore considered to be unsuitable, possibly due to variation of gamma in relation to *h*, invalidating the assumptions of this approach (Scott et al., 2013).

In order to estimate Ks, data on resting oxygen consumption for the following species was collected from the FishBase oxygen table Fishbase (2019): *S. aurata*, *A. anguilla*, *D. labrax*, *D. sargus*, *Labrus bergylta* and *C. labrosus*. This gave the metabolism in terms of O_2 consumption in mg/kg/h, which needed to be converted to grams of wet weight of prey needed to cover the standard metabolism and activity.

For this conversion the relation between body mass and resting metabolic rate presented in Clarke & Johnston (1999) was used to scale the oxygen consumption to that of a 1g fish.

Equation 2.4. Relation between resting metabolic rate (R_b) and body mass (M), with a being the constant and b the scaling exponent (Clarke & Johnston, 1999).

$$R_b(M) = a\, M^b$$

FishBase presents metabolic rate data as mgO_2/kg/h. This was converted to mmol of oxygen per fish per hour by dividing the mass of one mmol of oxygen in mg (32) and multiplying by the mass of the fish in kg *(M/1000)*.

Making *a* the subject of the metabolic scaling equation gives:

$$a = \frac{R_b(M)}{M^b}$$

Which can be used to give the metabolic rate for fish of 1g given in consumption of O_2 in mmol of O_2 h^{-1}. This was then converted to the weight of carbon needed for the respiration reaction to produce 1mmol of CO_2:

$$C = \frac{a * 12}{1000}$$

This mass of carbon was assumed to constitute half the dry weight. This was then converted to wet weight by dividing by 0.27 as in Gamito & Erzini (2005); as this is the rate per hour this was converted to rate per year by multiplying by 8760 (number of hours in a year).
Finally, Ks was estimated using the following:

$$Ks = C_{yr} * 1^{0.7}$$

With 1 referring to the mass of the individual in g (1g) and the units of Ks being $g_{(1-p/yr-1)}$.

However, these estimates proved so high that unrealistically high *h* and gamma values were needed before the model could reach steady state, also yielding impossible growth curves. This was due to extremely high food requirements to cover the metabolic rates predicted by the Ks estimates. These estimates were therefore considered unsuitable; there are several possible reasons for these unrealistic estimates, which are covered in the discussion section.
The metabolic rate was scaled to Wmat ($Ks_{(Wmat)}$) of each species using the following formula:

$$Ks_{(W_{mat})} = \frac{Ks(W_{mat}^{0.8})}{W_{mat}}$$

This method adjusts the Ks meaning that the species has at least enough food to reach its Wmat, allowing reproduction, which is necessary for reaching steady state. This gave much lower estimates and required much more realistic *h* and gamma values and produced sensible growth predictions. These were used for the final model.

In order to estimate the Ks value for species for which no O_2-consumption data was available, a linear regression between the know Ks values and the corresponding *h* values was conducted.

There was significant positive correlation between these parameters returning an *r* value of 0.894.

The linear regression:

$$Ks = -1.7525 + 0.4356 * h$$

This returned a P-value of 0.014 indicating a significant linear regression. However, it must be noted that this assumes Ks scales linearity with *h*.

Interaction matrix

The interaction matrix was left at all 1's for most species, except for those with specialist diets such as *M. barbatus* (FishBase, 2019). This is different from the diet matrix used by Gamito & Erzini (2005) in the Ecopath model, as this simply determines the proportions of each functional group in the diet of that particular species/functional group (Christensen et al., 2000). In size-spectrum modelling the diet of a predator is determined by prey size-selectivity and the availability of prey items in this size range, with the interaction matrix determining the relative probability of a predatory encounter (Scott et al., 2013).

This gave a predicted diet similar to the diet composition matrix in the Ecopath model from Gamito & Erzini (2005). Therefore, these parameters were considered to give a reasonably realistic representation of the diet composition for the species present.

For many of the predatory species the plankton interaction was reduced to 0.2, as setting this to 1 resulted in extremely high initial feeding levels due to the high plankton abundance. This resulted in an unrealistically high initial growth rate, which rapidly dropped when the individual grew out of feeding upon the plankton (resource) spectrum.

Closing the size-spectrum

As Gamito & Erzini (2005) isolated the lagoon and covered the surface with ropes preventing fishing, bird predation and immigration/emigration of large fish, making the assumption these parameters were not needed in model. However, in the size-spectrum model, not including these processes led to an unrealistic size-spectrum with large fish becoming more abundant due to low predation mortalities, as no predator present was large enough to feed upon them, resulting in a backwards curve with biomass becoming concentrated in the larger size classes.

This also prevented calibration of the abundance density, as the model predictions were much too low due to the size-spectrum predicting a smaller number of larger individuals, due to the biomass accumulating in the larger size-classes.

It was therefore considered necessary to include some degree of mortality/emigration to the larger size classes. Unfortunately, no data is available on fishing, immigration and emigration rates; therefore, to estimate this an artificial fishing pressure was introduced. The fishing effort was set to 1 as standard, with the L_{50} being set to just smaller than Wmat with the highest possible L_{25}-L_{50} value, this was to simulate the fact that fishing in the Ria Formosa is artisanal with often no attention being paid to minimum landing-sizes (personal observation). Furthermore, it is likely that emigration and mortality due to bird predation occurs of a range of size classes. The catchability of each species was increased, and the egg density increased until both the biomass and abundance densities were as similar as reasonably possible, as this changes the size-spectrum increasing the proportion of biomass in the smaller size-classes. Some species did not require any fishing pressure to balance the abundance densities, therefore the catchabilities were left at 0.

These theoretical fishing mortalities were converted to size-dependent natural mortalities, which were applied to the model. The fishing mortality was then returned to zero by setting the effort to zero.

Plankton

There is no way to directly input a plankton biomass value in MIZER; as the plankton spectrum is controlled by kappa (the carrying capacity of the resource spectrum), lambda (the exponent of the background spectrum) and the log^{10} plankton replenishment rate (Scott et al., 2013). We did not have any estimates for these, and they were therefore left at the default values.

Data on the biomass of plankton present in the lagoon was however available from Gamito & Erzini (2005), note that MIZER models both phytoplankton and zooplankton together unlike Ecopath which models them separately. The plankton biomass estimate was obtained by summing the biomass of phytoplankton and zooplankton and the predicted biomass of plankton was calculated using (PB = plankton biomass):

$$PB = npp * W_{full} * DW_{full}$$

(Scott et al., 2013)

Which gave the predicted biomass of plankton in each size class, these were then summed, giving the total predicted plankton biomass.

The actual biomass was then converted into wet weight, and could be used with the predicted biomass to calculate kappa using:

$$Kappa = \frac{actual\ biomass}{predicted\ biomass}$$

Which gave the value of 70.51318, with lambda being left at the default value of 2.08333 (Scott et al., 2013). Replicating the plankton groups in the Ecopath model as closely as possible.

No data on the maximum size of zooplankton or phytoplankton was provided by Gamito & Erzini (2005). Therefore the maximum size in plankton (zooplankton and phytoplankton, as these groups are pooled into the same size-spectrum in MIZER), was estimated using the diet composition of the species in the model, mostly using *S. aurata*, as making the assumption that when the individual reaches a weight of 10g, the proportion of plankton in the diet begins to fall rapidly, as the beta value results in plankton being too small to be preferentially selected for. This is consistent with previous reports of ontogenetic diet shifts in marine fish (Stoner & Livingston, 1984). The maximum plankton size was set at 0.0443g.

Ecopath model

The published Ecopath model from Gamito & Erzini (2005) was used for the comparison model. This model explicitly modelled two species *S. aurata* and *S. cantharus*, with the rest of the species represented by functional groups, with species grouping based upon result of stomach content analysis from Gamito et al., (2003). The invertebrate functional groups are the same in the size-spectrum model, however the Ecopath functional groups contain many species explicity modeled in the size-spectrum model (Table 2.2).

Table 2.2. Species modelled in the size-spectrum model with their corresponding functional group in the Gamito & Erzini (2005) model.

Species	Functional group
Dicentrarchus punctatus	pelagic and benthic feeding fish
Halobatrachus didactylus	pelagic and benthic feeding fish
Anguilla anguilla	pelagic and benthic feeding fish
Dentex dentex	pelagic and benthic feeding fish
Belone belone	pelagic and benthic feeding fish
Dicentrarchus labrax	pelagic and benthic feeding fish
Solea senegalensis	benthic feeding fish
Diplodus annularis	benthic feeding fish

Diplodus vulgaris	benthic feeding fish
Atherina cf. boyeri	benthic feeding fish
Mullus barbatus	benthic feeding fish
Diplodus sargus	benthic feeding fish
Sarpa salpa	benthic feeding fish
Engraulis encrasicolus	Planktonic feeding fish
Sardina pilchardus	Planktonic feeding fish
Chelon labrosus	Detritivorous feeding fish
Goby sp.	Small benthic feeding fish
Wrasse sp.	Small benthic feeding fish

Comparisons

Growth rates

The data set used for this model is fisheries independent, with Gamito & Erzini (2005) releasing the majority of fish after capture. For several of the more abundant species cohorts could be identified from size distribution histograms, which were used to get estimates of the actual growth rates of these species. This allows comparison with the growth rates predicted by the MIZER and Ecopath models. The species selected for analysis were: *S. aurata*, *S. cantharus* and *D. annularis*, as these were some of the most abundant species and clear cohorts could be visually identified in the size-frequency distributions. The von Bertalanffy parameters estimated from this were W_∞ and K(vb).

This analysis was conducted using the and FiSAT 2 (FAO-ICLARM Stock Assessment Tool) software package. The data was binned using 1 cm size bins, as FiSAT 2 uses length rather than weight; to obtain the size-frequency distributions for each sampling event, the individual length data from the samples was used.

Modal progression analysis using the Bhattacharya method (Bhattacharya, 1967) was performed; this gives an output where points on the graph corresponding to individual cohorts are manually selected. These are then grouped to allow estimation of the number of cohorts.

NORMSEP analysis (Tomlinson, 1971) was then performed using the results from the Bhattacharya analysis, the results of this were then saved as growth increment data.

This data was then used to estimate growth curves for the selected species using the ELEFAN 1 method (Pauly & David, 1981) and growth increment analysis using Munro's method (Munro & Pauly, 1983).

The returned L_∞ values were converted to W_∞ using the length to weight conversion from FishBase (2019):

$$W = a\,L^b$$

With species specific *a*/*b* estimates being obtained from FishBase (2019).

Weight-at-age-data was estimated from the size-spectrum model, then imported to FiSAT 2. This was then analysed to estimate the von Bertalanffy parameters predicted by the size-spectrum model. FiSAT 2 allows the use of weight rather than length for weight-at-age-analysis, therefore data was not converted to length. It was necessary to use FISAT 2 as MIZER does not re-estimate the von Bertalanffy depending upon the parameters used in the model.

The W_∞ and K(vb) parameters were estimated from the Ecopath model from Gamito & Erzini (2005). This was done by using life history parameters from FishBase (2019) for the species, then running a particle-size-distribution analysis, this returned W_∞ and K(vb) estimates for the functional groups. As two of these were species specific (*S. aurata* and *S. cantharus*), these estimates could be compared with those from MIZER and the raw data.

Diet matrix

The consumption of each prey species in the diet of each predator at each size class interval can be accessed from the model using the command:

- ➢ mizer::getDiet(params, n = params@initial_n, n_pp = params@initial_n_pp, B = params@initial_B, proportion =FALSE)

However to make this comparable with the Ecopath diet matrix, this must be summed over all size classes. This was done using the following command:

- ➢ rowSums(aperm(mizer::getDiet(params, proportion =FALSE), c(1,3,2)), dims = 2)

The consumption data was then converted to proportions by dividing the consumption of a particular prey group or speices by a predator by the total consumption of that predator. These were then summed again into the functional groups used in the Gamito & Erzini (2005) Ecopath model.

This gave the predicted diet composition over the entire life of the predator, this made comparison with Gamito et al., (2003) challenging, as this study did not include stomach data for the very small size-classes. Therefore a second diet composition matrix was created using diet composition when the predator species is at its Wmat. This was done in the same way, however only using consumption data from the Wmat size-class of each species.

Consumption/Biomass

A fundamental parameter for ecosystem level modeling is the quantity of food ingested (Q) by a population over a period of time (one year) relative to its biomass (B), or Q/B (Palomares & Pauly, 1998); however this is considered difficult to obtain, often being replaced by unreliable estimations, causing increased model uncertainty (Ainsworth & Walters, 2015). Considering growth in size-spectrum modeling is food dependent (Scott et al., 2013), estimation of this from the size-spectrum model is a convenient way of comparing trophic flows between the modeling metholodolgies.

Predicted estimates of individual consumption for each species at each size class within the ecosystem in the size-spectrum model, were obtained using the same commands as the diet matrix.

The abundance of the predator species by size-class was then extracted, which was then multiplied by the total consumption of an individual of that size-class, to get the total consumption by all individuals in that size-class. This was calculated for all size-classes then summed giving total consumption, which then was divided by the total biomass giving the Q/B ratio for the population.

Palomares & Pauly (1998) outlined methodologies for estimating Q/B from common life history parameters stating that Q/B estimates can be obtained from a single representative fish of that particular species. Using this concept, the individual consumption/individual biomass ratio was calculated, as this gave predicted ontogentic changes in the Q/B ratio over the life of the predator.

Production/Biomass

In Ecopath production refers to the elaboration of tissue by a group or species over the time period considered. Under the conditions assumed for construction of mass-balance models

Total mortality is equal to production/biomass (P/B); therefore this can be used as an input variable for estimation of P/B values (Christensen et al., 2000):

$Z = P/B$

Although the conditions of mass-balance have many similarities with the food-dependent growth fundamental to the size-spectrum workings, it is unlikey that Z = P/B applies to size-spectrum modeling.

Therefore, to estimate P/B, predictions of the growth of an individial of each species in each size class over a year (elaboration of tissue, or production), were multiplied by the abundance of individuals in each size-class, giving the total growth for that size-class, which was summed to give to total growth per year. This is the equivalent to total production in Ecopath, as it is the mass of tissue elaborated over the same time period (one year). This was divided by total biomass of that species or functional group, giving the estimates of P/B for the species present in the size-spectrum model.

The P/B estimates from the Ecopath model were obtained from Gamito & Erzini (2005).

Predation mortality

In Ecopath, predation mortality of a group or species (i) is the sum of the consumption of that group or species (i) by the other groups or species, divided by the biomass of that particular group (i). Predation mortality is calculated in Ecopath and is not an input parameter (Christensen et al., 2000).

In the size-spectrum methodology employed by MIZER, predation mortality is calculated so that the total consumption translates into corresponding predation mortalities on the ingested prey individuals of that particular size-class of the prey species (Scott et al., 2013). These estimations of predation mortality are therefore size-dependent.

Predation mortality estimates can be obtained from MIZER by using the getPredMort function in R. This gives the predicted predation mortality as for each species at each size class, which was used to generate predicted predation mortality curves for each species with size.

In order to calculate predation mortality estimates from the size-spectrum model comparable with those from the Ecoapth model, the predation mortality (proportion consumed by predators) of a particular species was summed across all size-classes divided by the total biomass of that group or species. This converts the predation mortalities as a function of size into the same format as the Ecopath estimates, allowing for comparison.

Chapter 3: Results

Size-spectrum model

Using the parameters displayed in (Table S1) (supplementary); steady state was reached, giving a multi-species size-spectrum of the Ria Formosa lagoon (fig 3.1).

The community size-spectrum (fig 3.1) represented by the black line follows a fairly linear decline in biomass density with increasing size, with some early fluctuations, until a sharp decline starting at approximately 650g. The early fluctuations in the community size-spectrum between 3.27x10^{-2} and 8.3g are due to many abundant species being grouped into the invertebrate functional groups, Annelida, Gastropoda, Bivalvia and Crustacea. This resulted in these four functional groups having a large influence on the community size-spectrum at that size range.

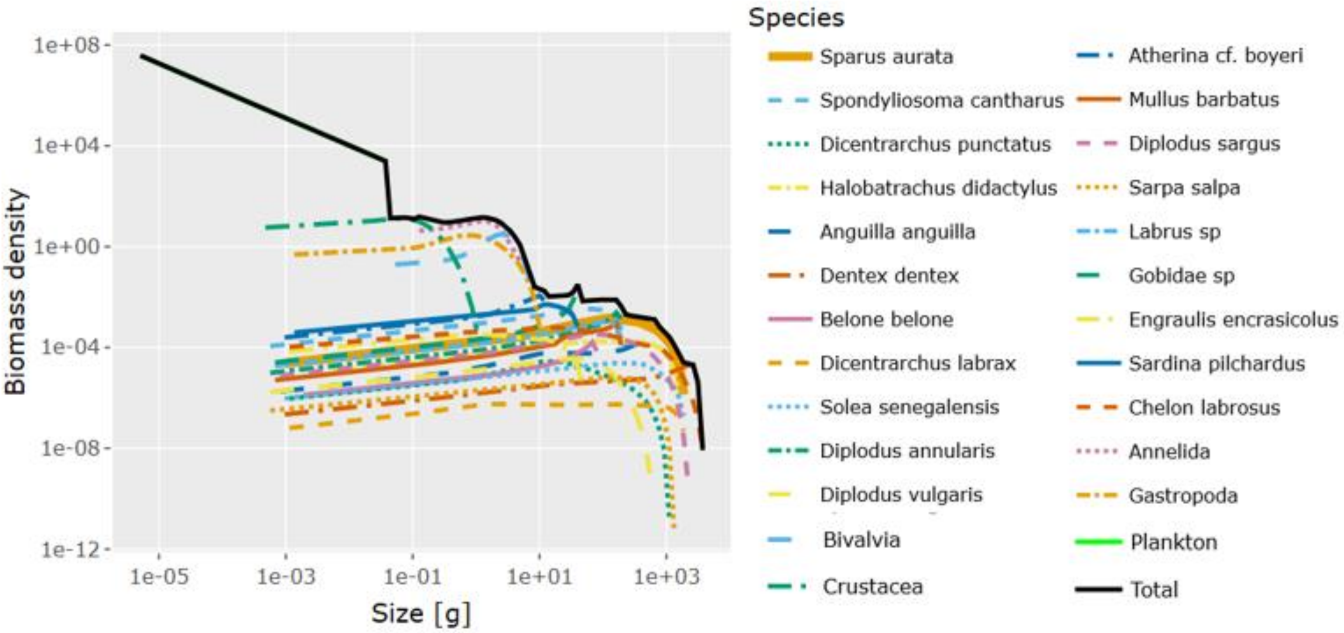

Figure 3.1. Multispecies size-spectrum of the Ria Formosa lagoon community. All weights are wet weights, biomass density is in g per m^2 wet weight. Scale is constant.

The size-spectrum is relatively flat with little decline in biomass density from 16.7g to 650g, which was then followed by a rapid decline. This is likely due to the declining feeding level with increasing size (fig 3.4), with the larger species becoming food limited above this size, as well as many of the smaller species reaching their maximum size before this point (fig 3.5).

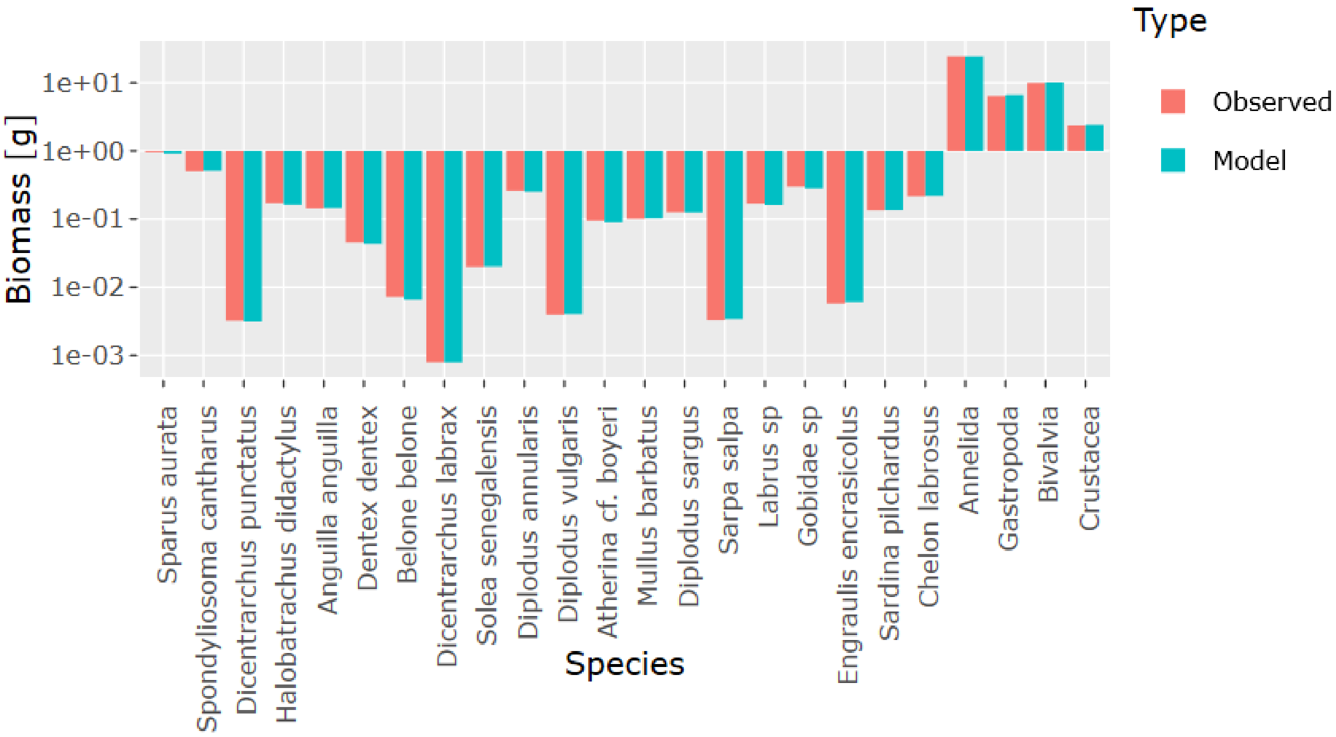

Figure 3.2. Observed and predicted biomass of the species and functional groups present in the size-spectrum model.

The size-spectrum model parameters were tuned to predict biomasses as closely as possible for the species and functional groups present (Fig 3.2). The invertebrate functional groups have the largest biomasses followed by *S. aurata* and *S. cantharus* with the largest biomass of the fish. The Goby sp and Wrasse sp also have high biomasses, which is due to these groups being comprised of many abundant species. Generally, the Biomass density appears to decline with increasing W_∞ and trophic level (fig 3.2), with *D. labrax* having the lowest biomass density, followed by *D. punctatus*.

D. dentex has a higher biomass density than *D. punctatus* and *D. labrax* despite having a much larger W_∞, which was due to very few *D. punctatus*, *D. labrax* and *D. dentex* being present in the sample, with the *D. labrax* and *D. punctatus* comprising a few small individuals. Only a single *D. dentex* of 961.3g was sampled, which caused this species to have a much higher biomass density, despite a very low abundance. Many other species present in low biomasses were very infrequent during the sampling, except for *D. vulgaris*, which had a low average size. In fact many species present have low biomass and abundance densities (figs 3.2 and fig 3.3).

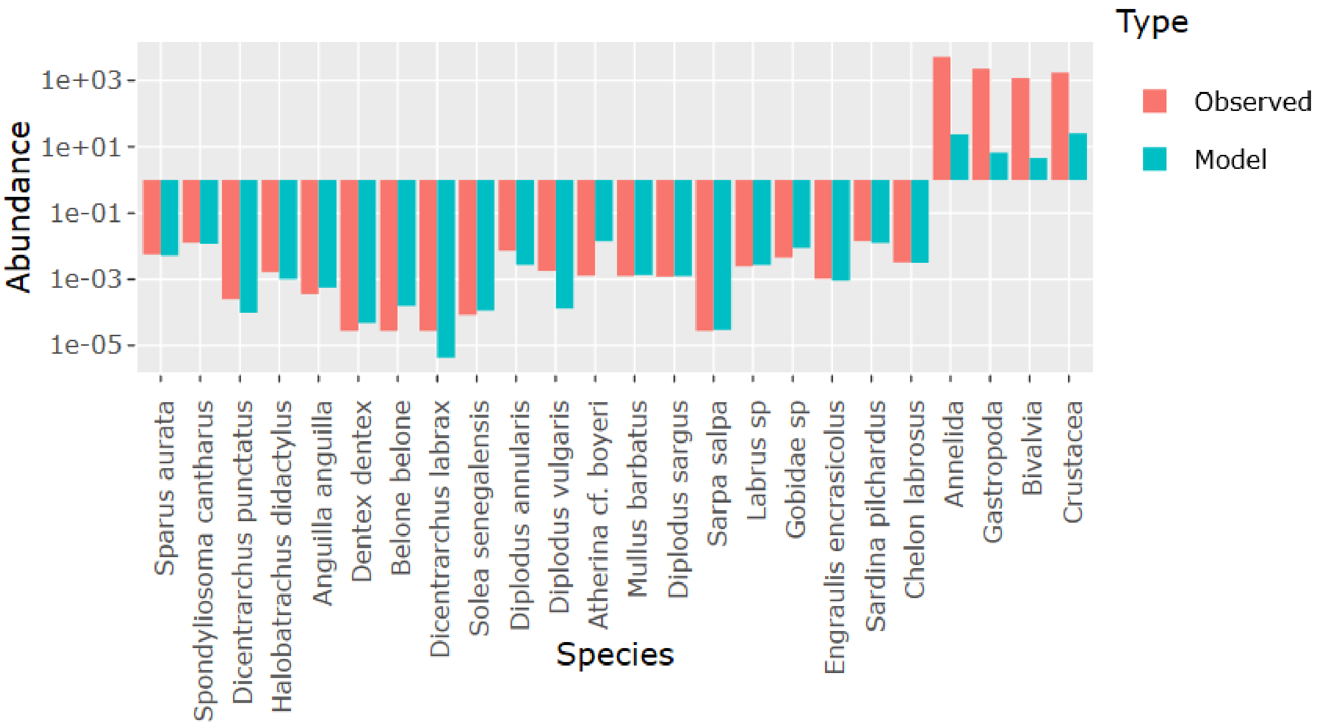

Figure 3.3. Observed and predicted abundances of species and functional groups present in the model.

The parameters were tuned so the predicted abundance matched the actual abundance as closely as possible. However this proved more dificut than tuning the biomass estimates and there is high variability in the discrepancies between the predicted and actual abundances (fig 3.3).

These discrepancies were minimal for the more abundant species such as *S. aurata*, *S. cantharus* and *M. barbatus*, which were also present over a wide size-range in the sample data. The abundances of these species required only small adjustments to the parameters controlling the size-structure, as larger individuals with a lower abundance for the same biomass, therefore the size-structure can be changed by altering the parameters responsible for mortality and growth rate.

However for some species present in very small numbers, such as *D. labrax*, *D. punctatus*, and *D. dentex*, or present only in small sizes such as *D. vulgaris* and *D. punctatus*, it was not possible to tune these exactly, as the parameters needed to be adjusted to unrealistic values which prevented the model from reaching steady state.

There is a huge discrepancy between the predicted and actual abundances of the invertebrate groups: Annelida, Gastropoda, Bivalvia and Crustacea. This means that the predicted mean size of these invertebrate groups is much larger than the actual mean size, which is clearly seen in their dramatically lower modelled abundances (fig 3.3). This was necessary for the functioning of the model, as due to the low fish biomass there is a low abundance of larger prey items (figs 3.2 and 3.3). If the mean size was decreased so the modeled and actual abundances were the same, there would not be sufficient prey in the larger size-classes for many of the fish to reach maturity. This was concluded when attempting to further increase the abundance (therefore reducing the size), which led to a parameter set unable to reach steady state, as the predators did not have enough prey to cover their metabolic cost. This phenominon is still apparent even with the final parameter set as can be seen in the declining feeding level with increasing size (fig 3.4).

Feeding parameters

The initial feeding levels were kept around 0.6, as this is considered the default value for most species (fig 3.4); for most species this declined with size, with this trend being more pronounced for species with high W_∞ and low beta values, as they prefer larger prey. Some of the larger predators with low beta value such as *D. labrax* and *D. dentex* have a hump in the declining feeding level with a small increase in feeding level. This occurred across the size-classes 2g – 380g in *D. labrax* and is very pronounced; these are likely due to the main prey items for most predators being the invertebrates, which have a high biomass and also suffer from biomass accumulation in the larger size-classes for these groups (fig 3.1).

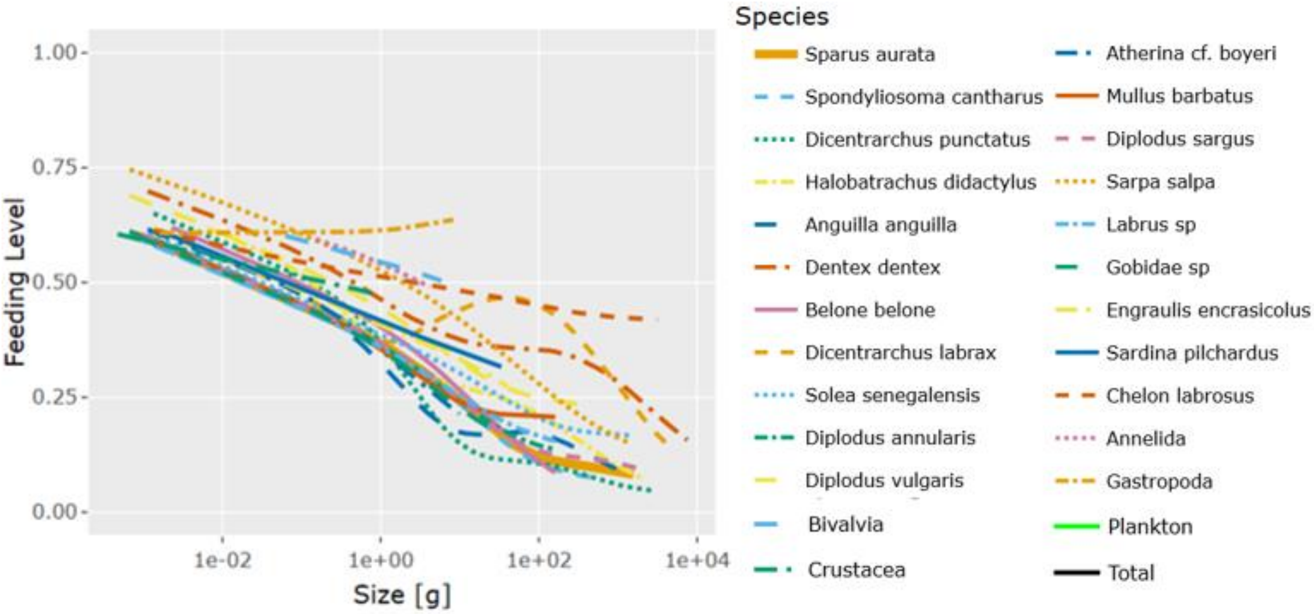

Figure 3.4. Feeding levels with size for the species and functional groups present in the model.

This biomass accumulation led to an increased availability of prey in these size classes. However, once the predator grows sufficiently large that these invertebrate groups are mostly out of the prey-size-selection range, there appears to be a decline in the availability of prey items, likely due to the low biomass of fish in the system and low W_∞ of the invertebrate groups.

The feeding level of the gastropods in fact increases, this appears to be due to this group preying on the other invertebrate functional groups; as the individual grows the more of these prey items are in the prey-size preference of the snails, causing an increasing feeding rate (fig 3.4).

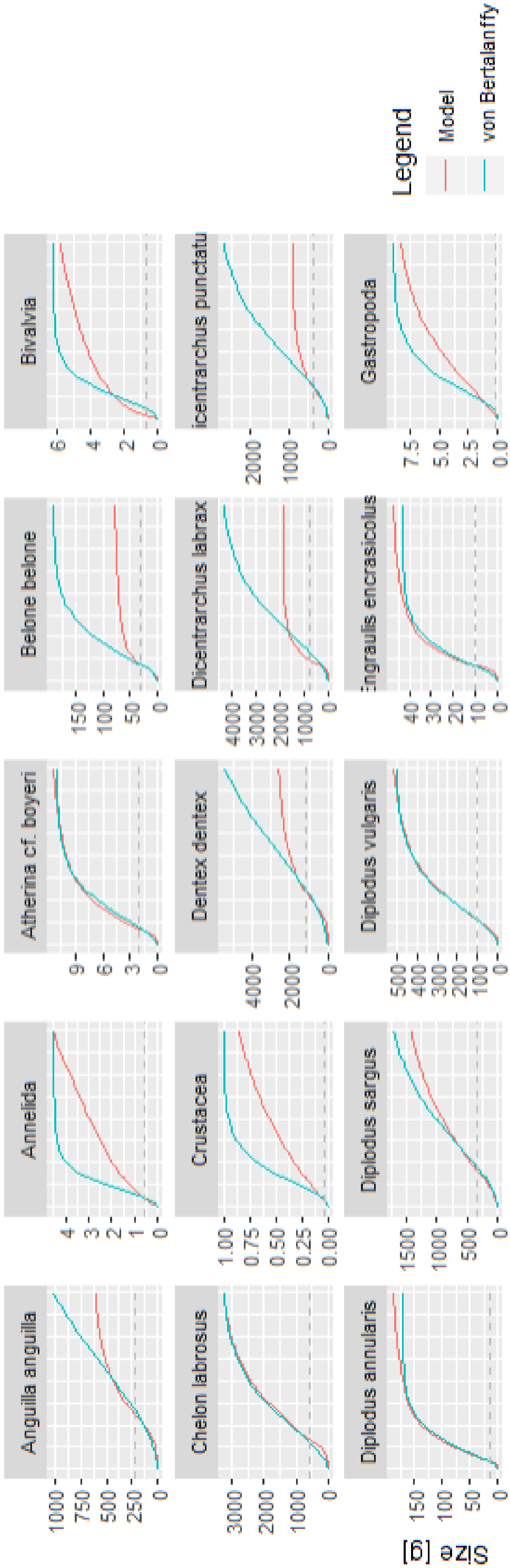
Anguilla anguilla
Annelida
Atherina cf. boyeri
Belone belone
Bivalvia
Chelon labrosus
Crustacea
Dentex dentex
Dicentrarchus labrax
icentrarchus punctatu
Diplodus annularis
Diplodus sargus
Diplodus vulgaris
ngraulis encrasicolus
Gastropoda
Gobidae sp
alobatrachus didactylu
Labrus sp
Mullus barbatus
Sardina pilchardus
Sarpa salpa
Solea senegalensis
Sparus aurata
ondyliosoma canthar
Size [g]
Age [years]
0
5
10
15
20
Legend
Model
von Bertalanffy

Figure 3.5. Growth rates predicted by the model compared with those generated using von Bertalanffy parameters from Fishbase (2019).

Many of the species present in the model cannot grow until their W_∞ (fig 3.5); this trend is most apparent for the larger predatory species with high W∞ and beta values, such as *D. dentex* and *D. labrax*. Many species have growth curves similar to the von Bertalanffy estimates, such as *M. barbatus*, *C. labrosus*, *D. vulgaris* and *S. aurata*.

The invertebrate groups were given estimated growth curves based on known parameters, which were then altered based upon the abundance predictions (fig 3.3). In order to try to make a life history which represented a range of species, a lower than normal Wmat and a much higher W_∞ with the growth rate being lowered by lower M values, in order to predict a wide range of sizes.

D. labrax has a very strange and unrealistic growth curve with slow growth in the early stages being followed by a rapidly increasing then decreasing growth rate (fig 3.5). This was attributed to the increase in feeding level in this size range, resulting in an elevated growth rate during this period.

Parameter estimation and calibration

The beta estimates derived using the allometric relationships for a predators mouth area as a function of its length presented in Karachle & Stergiou (2011), gave a wide range of beta values (17-1844) (table 3.1; fig 3.6).

Table 3.1. Beta estimates derived from the relationships presented by (Karachle & Stergiou 2011).

	Beta		Beta
S. aurata	399	*D. vulgaris*	400
S. cantharus	394	*A. cf. boyeri*	55
D. punctatus	49	*M. barbatus*	148
H. didactylus	24	*D. sargus*	403
A. anguilla	47	*S. salpa*	1319
D. dentex	151	*labrus sp*	392
B. belone	671	*Gobidae sp*	179
D. labrax	41	*E. encrasicolus*	52
S. senegalensis	1844	*S. pilchardus*	17
D. annularis	317	*C. labrosus*	286

S. pilchardus was predicted to select for the largest relative prey size, with a beta value of 17 with S. senegalensis selecting for the smallest prey with a beta value of 1844 (table 3.1).

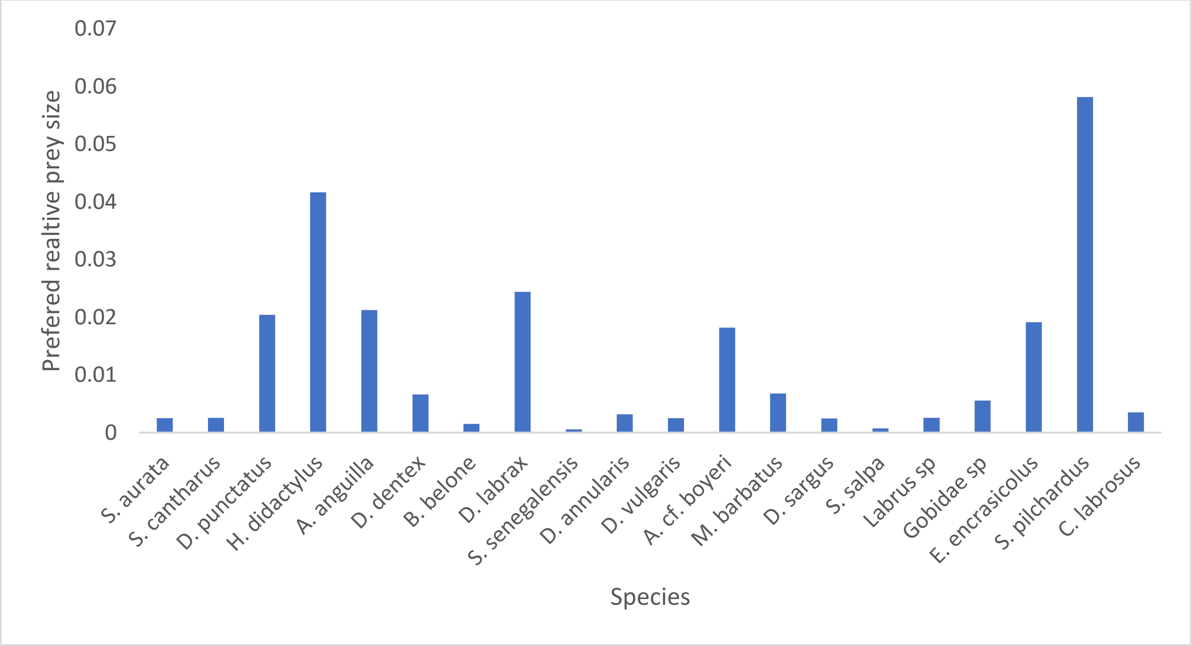

Figure 3.6. preferred prey size for each predator species as a proportion of their body mass, values refer to 1/beta, as it allows better visual representation.

Additional size-dependent mortalaity

Figure 3.7 shows the size-spectrum for the lagoon community when no additional size-dependent mortality (which was used to attempt to include some measure of emmergration, fishing and bird predation), which are the same assumptions made by Gamito & Erzini (2005). This led to a similar size-spectrum to that with the additional mortality shown in in fig 3.1; however there was a greater accumulation of biomass towards the upper size class, which suggests the size-spectrum to have a high number of large individals, compared with the number of smaller individuals (fig 3.7).

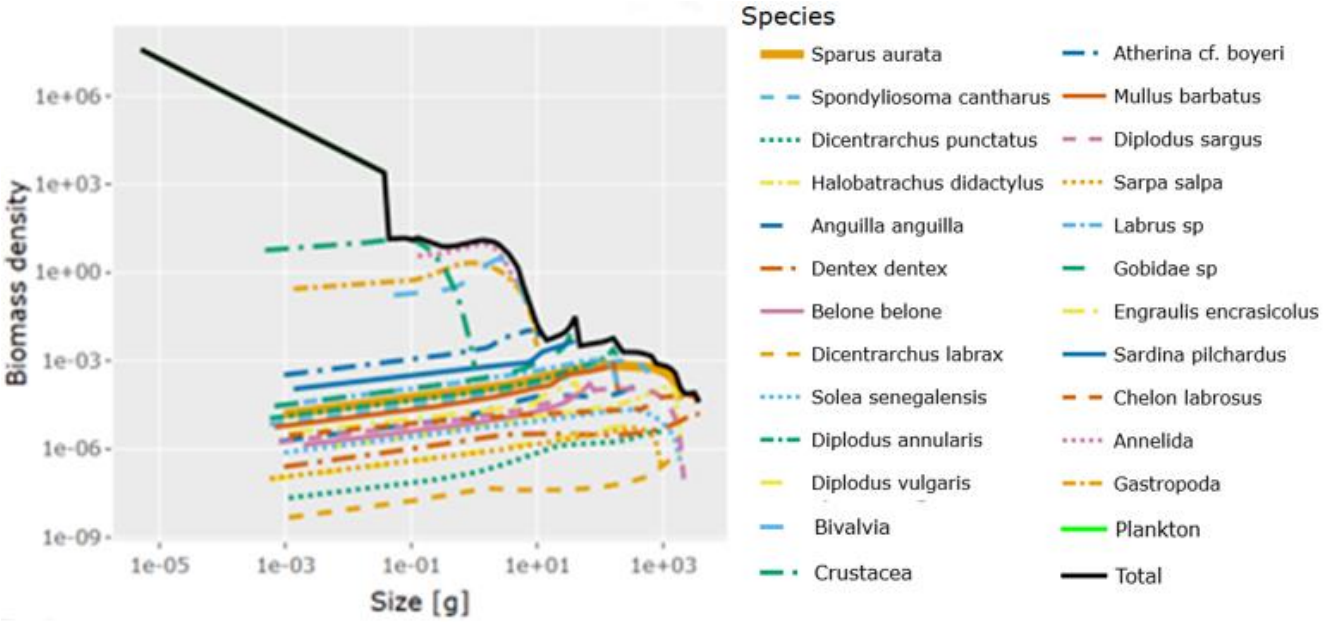

Figure 3.7. Multispecies size-spectrum of the Ria Formosa lagoon community, without additional size-dependent mortality. Biomass density is in g per m^2 wet weight. Scale is constant.

Figure 3.8 shows the predicted and actual abundances of the species and functional groups present. The abundances are generally lower than those predicted in figure 3.3; however, for some species the predictions were similar, as size-dependent mortality was not added to all species/functional groups.

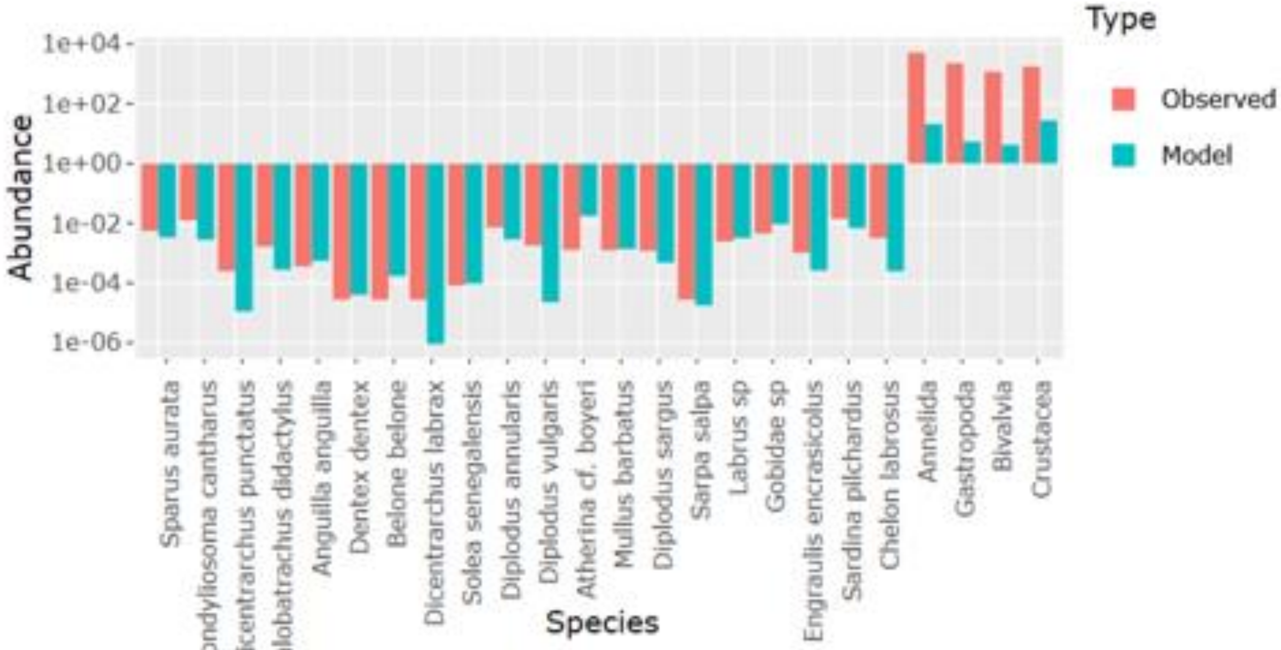

Figure 3.8. Observed and predicted abundances of species and functional groups present in the model, when no additional size-dependent mortality was added.

Comparisons

Growth

There were large differences between W_∞ estimates from weight-at-age data from the size-spectrum model, the sample data, Ecopath and the FishBase estimates, with Ecopath consistently predicting the lowest values (figs 3.9 & 3.10)

MIZER predicted higher W_∞ than the data estimate for *S. aurata*, however predicted lower W_∞ than the data for *S. cantharus* and *S. aurata* (fig 3.9).

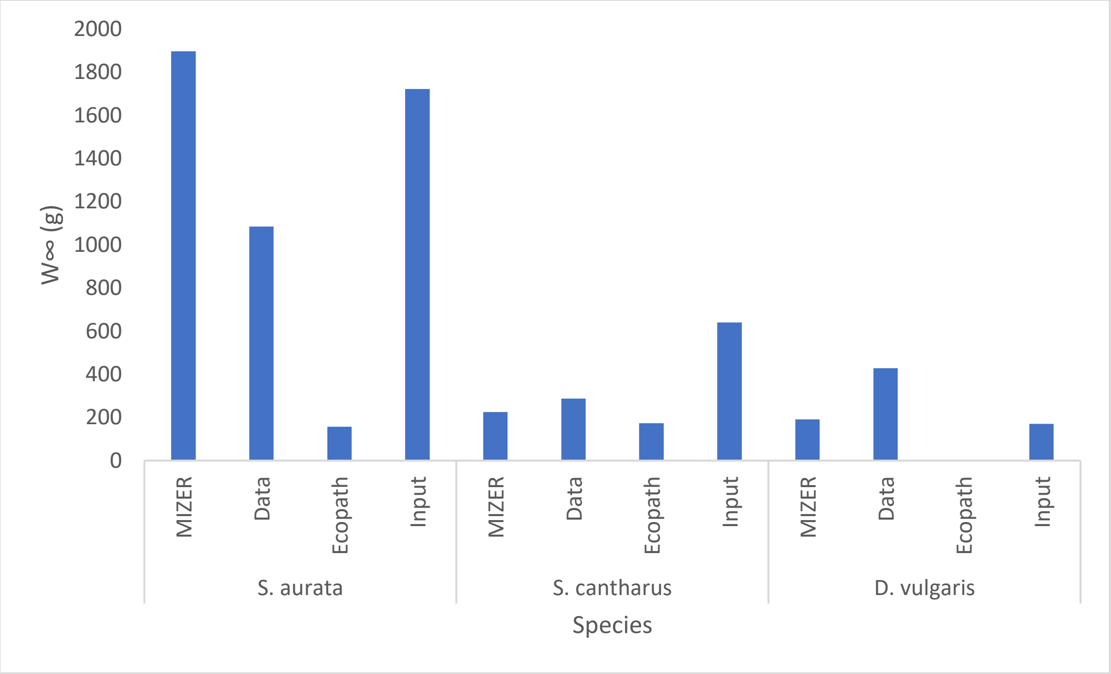

Figure 3.9. Bar chart comparing the W_∞ predicted from MIZER estimates, cohort analysis of the raw data, Ecopath estimates from the Gamito & Erzini (2005) model and the input parameter from FishBase (2019).

There was a high variability in the estimations of K(vb) for *S. aurata*, with the size-spectrum data giving a low of 0.09 and the estimate from the data giving a high of 0.56 (fig 3.10). However, *S. cantharus* had K(vb) estimates from MIZER, Ecopath and FishBase of 0.3, but the estimate from the data was much lower at 0.12. The cohort analysis gave a slightly lower K(vb) estimate of 0.26 for *D. vulgaris* compared with 0.2 from MIZER, however these were both much lower than the FishBase value of 0.47. No estimate for *D. vulgaris* growth parameters was available from Gamito & Erzini (2005).

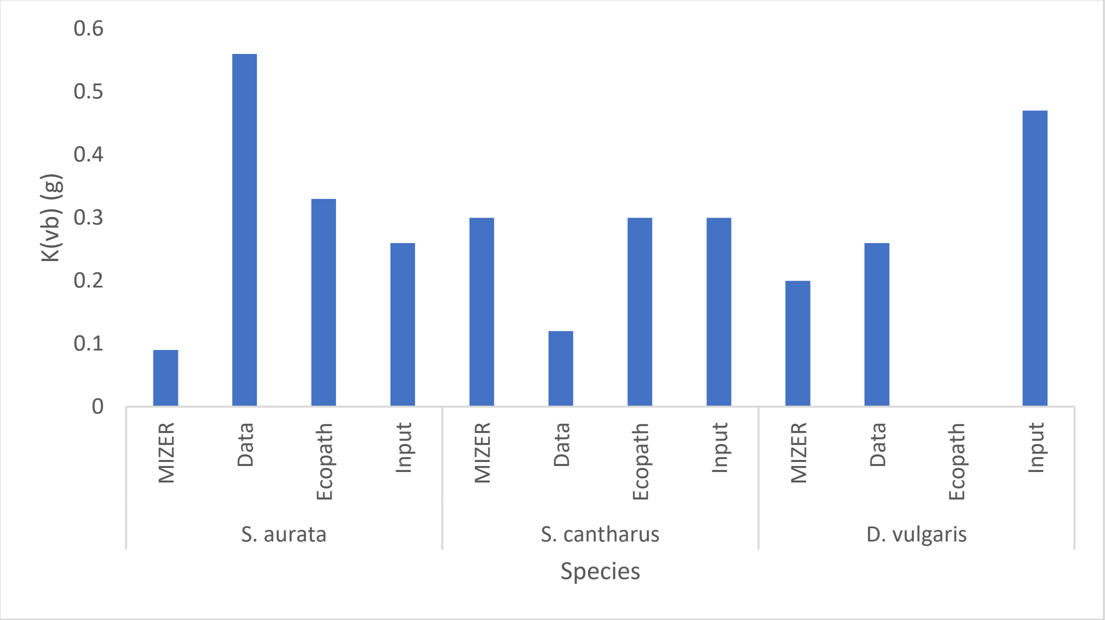

Figure 3.10. Bar chart comparing the K(vb) predicted from MIZER estimates, cohort analysis of the raw data, Ecopath estimates from the Gamito & Erzini (2005) model and the input parameter from FishBase (2019).

Diet proportions

Table 3.2 shows the mean proportions of each prey species diet of a predator across all size classes. The diets of all species include a high proportion of plankton and detritus, which represents the largest difference between the predicted diet compositions of the size-spectrum model and Ecopath (Table 3.4).

The diets of many fish functional groups contain a high proportion of plankton, even if they are not considered strict planktivores, such as *S. cantharus*. The remainder of the diet is comprised mostly of the invertebrate functional groups Annelida, Gastropoda, Bivalvia and Crustacea, followed by detritus. The fish functional groups made up only a small portion of the diets of the predators, with *S. aurata* and pelagic-benthic feeding fish displaying the highest degree of piscivory.

Table 3.2. The proportions of each prey species or functional group making up the diet composition of the predator summed across all size classes.

Predator/Prey		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
S. aurata	**1**	0.0011	0.0024	0.0004	0.0029	0.0028	0.0019	0.0005	0.2645	0.1427	0.2225	0.0259	0.1927	0.1396
S. cantharus	**2**	0.0000	0.0002	0.0000	0.0003	0.0002	0.0002	0.0000	0.0828	0.0454	0.0509	0.0211	0.5696	0.2294
Pelagic-benthic ff	**3**	0.0111	0.0117	0.0036	0.0119	0.0113	0.0041	0.0030	0.3931	0.1161	0.2230	0.0113	0.0447	0.1551
Benthic ff	**4**	0.0006	0.0013	0.0002	0.0016	0.0014	0.0010	0.0003	0.2466	0.1042	0.1478	0.0299	0.3151	0.1501
Small b-p ff	**5**	0.0001	0.0002	0.0000	0.0003	0.0002	0.0002	0.0000	0.1509	0.0417	0.0471	0.0236	0.5605	0.1752
Planktonic f	**6**	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0005	0.0002	0.0001	0.0007	0.8885	0.1101
Detritivorous f	**7**	0.0001	0.0002	0.0000	0.0002	0.0002	0.0002	0.0000	0.0086	0.0082	0.0105	0.0042	0.0441	0.9235
Annelida	**8**	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0007	0.0002	0.0001	0.0011	0.3844	0.6135
Gastropoda	**9**	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0412	0.0120	0.0091	0.0144	0.0000	0.9232
Bivalvia	**10**	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0004	0.0000	0.0001	0.0003	0.4892	0.5101
Crustacea	**11**	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0009	0.0004	0.0001	0.0022	0.3603	0.6362
Plankton	**12**													
Detritus	**13**													

The diet composition assuming the individual is at its Wmat was also estimated (table 3.3), which removes the influence of ontogenetic diet shifts that have been documented for many species (Stoner & Livingston, 1984; Wells et al., 2008). Benthic-pelagic feeding fish had a higher proportion of plankton and a lower degree of piscivory, compared with the diet proportions as a function of all size-classes. However, for many of the other species the proportion of plankton consumed was lower, with a similar decrease in piscivory. The invertebrate functional groups still appear to comprise the largest proportion of the diets.

Table 3.3. The different proportions of prey species in the diet of the predator species or functional group at the Wmat predicted by the MIZER model.

Predator/Prey		1	2	3	4	5	6	7	8	9	10	11	12	13
S. auratus	1	0.0003	0.0010	0.0000	0.0002	0.0006	0.0006	0.0003	0.2971	0.1598	0.2149	0.0371	0.1495	0.1360
S. cantharus	2	0.0000	0.0002	0.0000	0.0000	0.0001	0.0001	0.0000	0.1118	0.0613	0.0655	0.0283	0.4464	0.2858
Benthic-pelagic ff	3	0.0059	0.0082	0.0003	0.0012	0.0042	0.0018	0.0018	0.2971	0.1027	0.2094	0.0051	0.1537	0.1943
Benthic ff	4	0.0001	0.0003	0.0000	0.0001	0.0002	0.0002	0.0001	0.1699	0.0728	0.0828	0.0366	0.4961	0.1402
Small-benthic ff	5	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0898	0.0254	0.0241	0.0225	0.6859	0.1520
Planktonic ff	6	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0002	0.0001	0.0000	0.0004	0.8969	0.1025
Detritivorous f	7	0.0000	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0070	0.0068	0.0070	0.0057	0.0591	0.9141
Annelida	8	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0001	0.0000	0.0000	0.0006	0.4745	0.5248
Gastropoda	9	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0004	0.0004	0.0000	0.0048	0.0000	0.9945
Bivalve	10	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0001	0.5437	0.4562
Crustacea	11	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0001	0.4644	0.5354
Plankton	12													
Detritus	13													

There are some clear differences between the diet compositions predicted by Ecopath (Table 3.4) compared with those obtained from the size-spectrum model, most significantly that plankton is not present in the diet of many of the fish species in the Ecopath diet matrix, but comprises a major portion of the diet of most species in the size-spectrum model (table 3.2). The proportion of the fish and invertebrate functional groups in the diet is lower for all species in the MIZER model.

Table 3.4. Diet composition matrix in relative biomass of prey groups for the Ecopath model of the Ria Formosa lagoon (adapted from Gamito & Erzini, 2005).

Predator/Prey		1	2	3	4	5	6	7	8	9	10	11	12	13
S. aurata	1	0.0110	0.0200	0.0500	0.0200	0.0140	0.1050	0.0060	0.2460	0.2690	0.0520	0.2070	0.0000	0.0000
S. cantharus	2	0.0050	0.0050	0.0070	0.0050	0.0040	0.0100	0.0030	0.1030	0.8200	0.0360	0.0020	0.0000	0.0000
Benthic-pelagic ff	3	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.5410	0.1270	0.0440	0.2880	0.0000	0.0000
Benthic ff	4	0.0000	0.0000	0.0010	0.0010	0.0000	0.0010	0.0000	0.4900	0.0120	0.0070	0.4880	0.0000	0.0000
Small-benthic ff	5	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9500	0.0500
Planktonic ff	6	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1000	0.1000	0.0500	0.0600	0.6400	0.0500
Detritivorous f	7	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1000	0.1000	0.1000	0.0700	0.0000	0.6300
Crustacea	8	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.5000	0.5000
Gastropoda	9	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0050	0.0050	0.0300	0.0100	0.7500	0.2000
Bivalvia	10	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0050	0.0040	0.0110	0.0100	0.1900	0.7800
Annelida	11	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0500	0.0500	0.0600	0.1200	0.0000	0.7200
Plankton	12													
Detritus	13													

There are some clear differences between the diet compositions predicted by Ecopath (Table 3.4) compared with the size-spectrum model, most significantly that plankton is not present in the diet of many of the fish species in the Ecopath diet matrix, but comprises a major portion of the diet of most species in the MIZER model (Table 3.2).

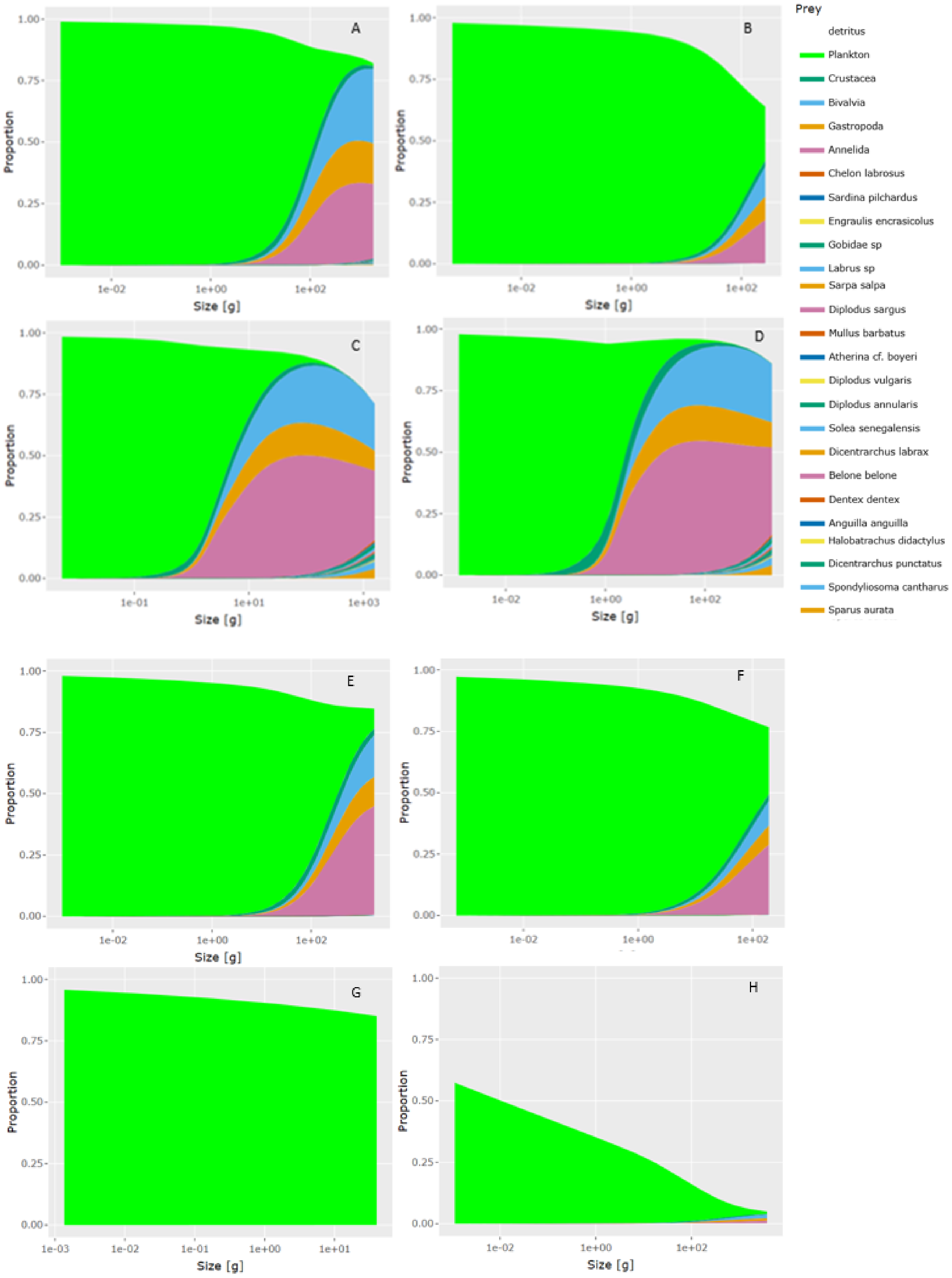
A
B
C
D
E
F
G
H
Proportion
Size [g]
0.00
0.25
0.50
0.75
1.00
1e-03
1e-02
1e-01
1e+00
1e+01
1e+02
1e+03
Prey
detritus
Plankton
Crustacea
Bivalvia
Gastropoda
Annelida
Chelon labrosus
Sardina pilchardus
Engraulis encrasicolus
Gobidae sp
Labrus sp
Sarpa salpa
Diplodus sargus
Mullus barbatus
Atherina cf. boyeri
Diplodus vulgaris
Diplodus annularis
Solea senegalensis
Dicentrarchus labrax
Belone belone
Dentex dentex
Anguilla anguilla
Halobatrachus didactylus
Dicentrarchus punctatus
Spondyliosoma cantharus
Sparus aurata

Figure 3.11. Diet composition as a function of size from the MIZER model for eight species/functional groups: a – S. aurata, b – S. Cantharus, C - H. Didactylus, D - D. Labrax, E - S. Senegalensis, F- labrus sp, G - S. Pilchardus, H – C. Labrosus. Detritus has no colour.

The diets of the species varied greatly with the predator size (fig 3.11), with almost all species having plankton make up the majority of the diet during the small size classes. The exception is gastropods as these do not feed upon plankton, with detritus comprising the majority of the diet. As the predators grew the proportion of plankton declined with an increase in detritus consumption with the main prey groups becoming Annelida, Gastropoda, Bivalvia and Crustacea. For the larger predator species, the proportion of fish in the diet increased and the proportion of invertebrates decreased towards the maximum size of the predator.

Total Mortality

Figure 3.12 shows the total mortality as a function of size. There appears to be size-dependent change in the total mortality rate with size; the total mortality of the invertebrate functional groups increases with size to a peak at about 0.01g, which then decreases until these reach their maximum size. The fish species and functional groups follow similar trends with most species showing maximum predation mortalities at around 1g with a much less pronounced curve. At around this point the total mortality for some species starts to increase dramatically; this is a product of the additional size-dependent mortality applied to the size-spectrum model.

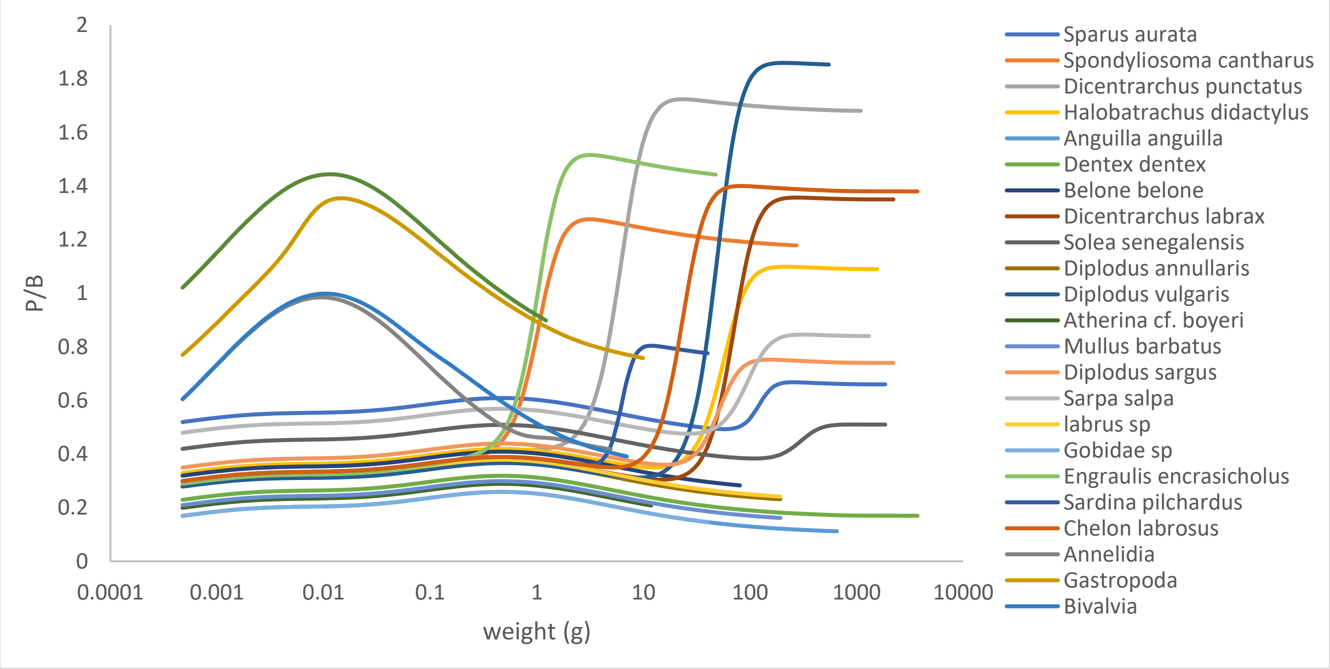

Figure 3.12. P/B (total mortality) for the species/functional groups present in the MIZER model as a function of individual body size. The x-axis is a logarithmic scale.

Consumption/Biomass

Estimates of Q/B calculated from predicted consumption from the size-spectrum model and the Ecopath model by Gamito & Erzini (2005) are presented in Table 3.5.

This returned some unexpected results, with some species or functional groups giving estimates reasonably similar to those from Ecopath. For example *S. aurata* and *S. cantharus*, whereas other Q/B estimates are impossibly high, such as Benthic-pelagic ff with estimated Q/B ratio from the size-spectrum data of 2227.78, which is completely unrealistic.

Table 3.5. Original consumption over biomass estimates from the size-spectrum model and the Ecopath model from Gamito & Erzini (2005). ff refers to feeding fish.

Functional group	**Q/B (MIZER)**	**Q/B (Ecopath)**
S. aurata	6.05	4.91
S. cantharus	4.87	4.6
Benthic-pelagic ff	2227.76	6.06
Benthic ff	236.99	4.66
Small-benthic ff	2.35	28.51
Planktonic ff	20.85	16.587
Detritivorous f	57.50	9
Annelida	0.00096	7.5
Gastropoda	0.015	30
Bivalvia	0.0075	30
Crustacea	0.0025	15

This was due to an error in the original calculation, as this is a resubmission, the corrected Q/B and P/B results will be used as the original are for a singling individual, not the population as a whole and are thus not comparable to the Ecopath estimates. However, the finding that the biomass and abundance density have a significant influence on the predictions suggests a possible issue with the model working and these results should not be ignored.

The Ecopath Q/B ratios are generally higher than the estimates from the size-spectrum model (fig 3.13). The size-spectrum model also predicted *S. aurata* to have the highest Q/B ratio of the fish species, with most having low ratios. These differences are most extreme in the invertebrate functional groups, planktonic ff and small benthic-pelagic ff. There is some similarities with both methodologies predicting the highest ratios for the invertebrate functional groups.

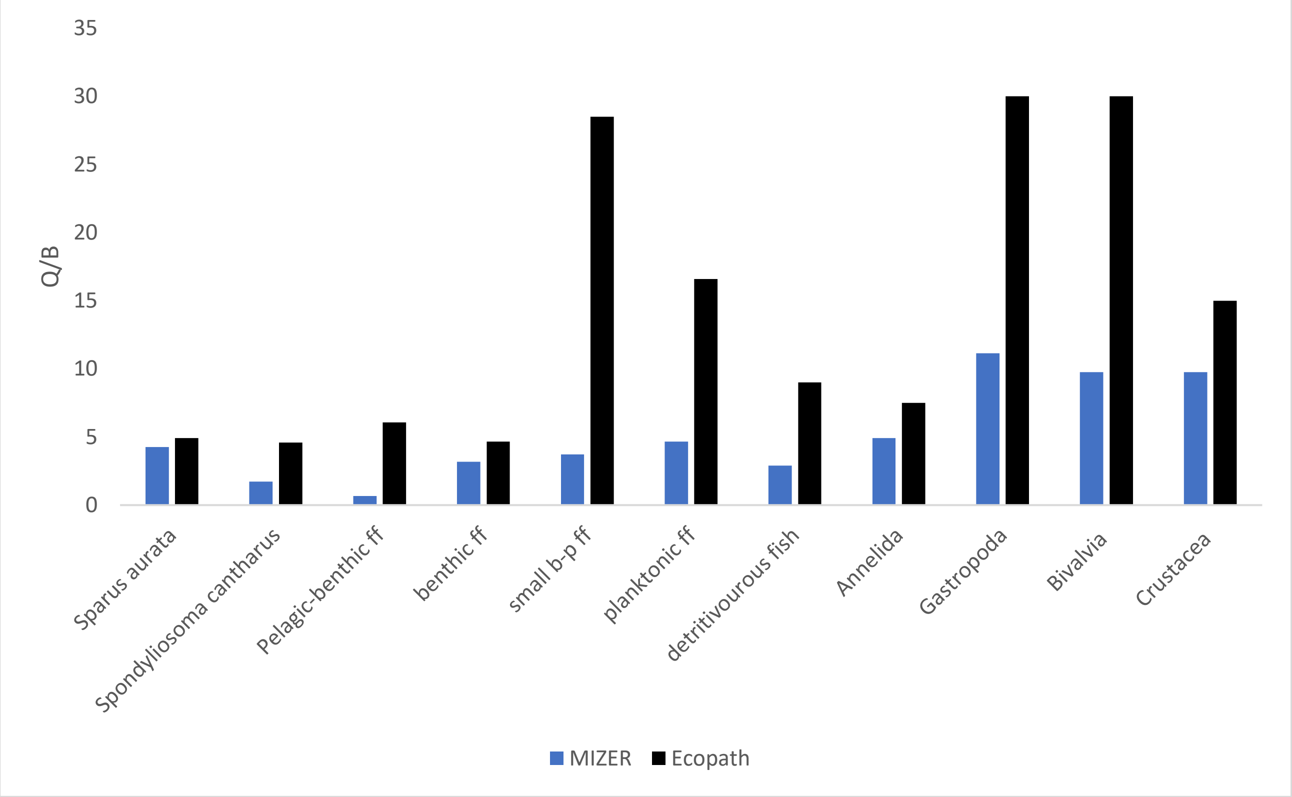

Figure 3.13. Comparison of the corrected Q/B estimates estimated from MIZER and the Ecopath estimates from Gamito & Erzini (2005).

The Q/B ratios for and individual of each size class for several species are shown in fig 3.14. There are extremely large differences between the minimum and maximum sizes, with *S. aurata* having an initial Q/B ratio of 270, which declined to 2. This trend is less exaggerated for lower trophic level species such as Annelida, which has a Q/B ratio of 9 at the smallest size classes, declining to less than 4, which is a much smaller range of Q/B ratios.

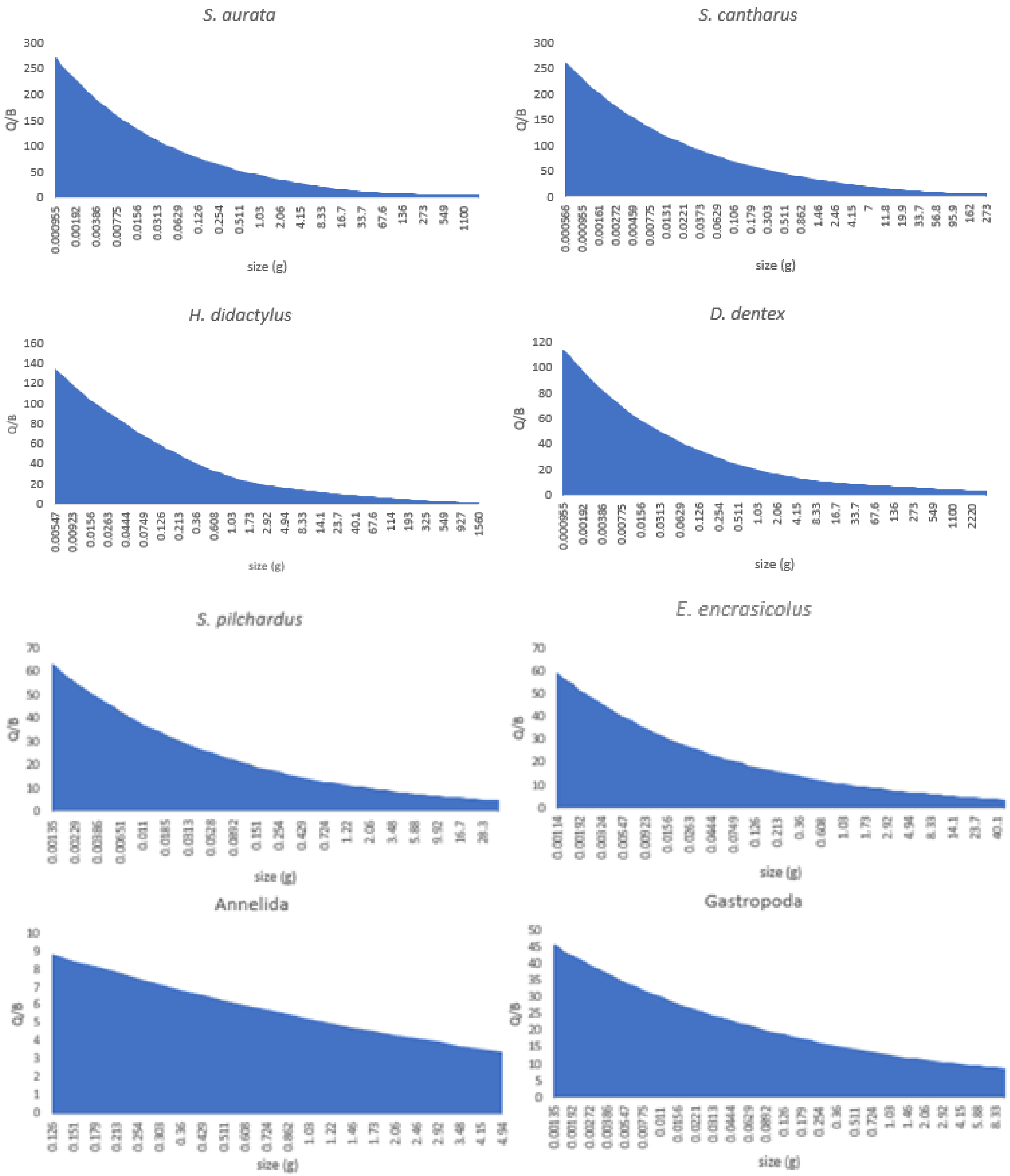

Figure 3.14. Area graphs showing the predicted Q/B ratios for each size class of eight species estimated from the MIZER model.

Production/Biomass

The P/B values were also corrected and the updated results are presented. The original estimates are presented in table 3.6, these appear to have the opposite trend to the original Q/B, with the invertebrates having excessively high ratios and the fish species having excessively low ratios.

Table 3.6. P/B estimates obtained from the size-spectrum model and the Ecopath model.

Functional Group	**MIZER P/B**	**Ecopath P/B**
S. auratus	0.073	0.41
S. cantharus	0.089	0.52
Benthic-pelagic ff	0.13	0.63
Benthic ff	0.097	0.46
Small-benthic ff	0.12	0.89
Planktonic ff	0.095	1.815
Detritivorous f	0.0047	0.28
Annelida	381.21	1.99
Gastropoda	45.14	4.20
Bivalve	55.85	2.53
Crustacea	467.78	4.43

The corrected results predicted lower P/B ratios from the size-spectrum model for all species except *S. aurata* (fig 3.15). The differences were greatest for planktonic ff and the invertebrate groups, both models predicted the highest P/B ratios for the invertebrate groups.

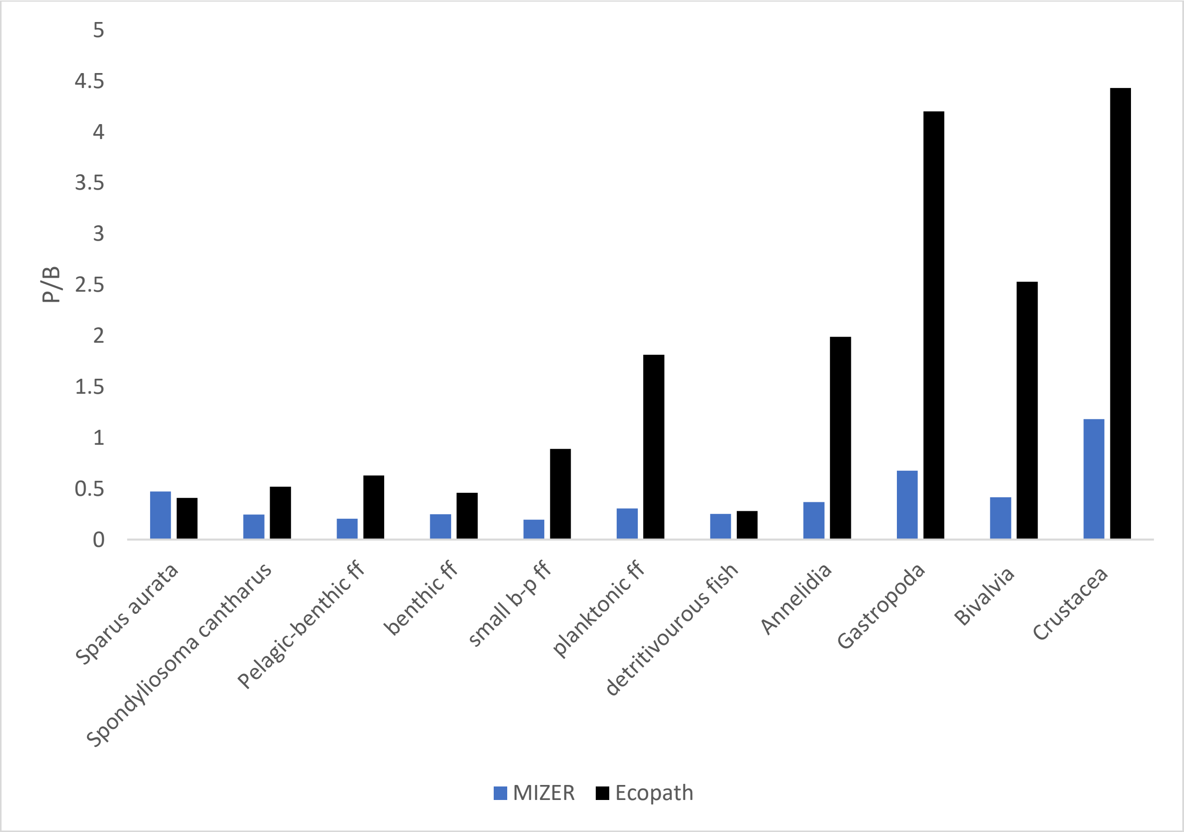

Figure 3.15. Bar chart comparing the corrected P/B estimates from the size-spectrum model and the Ecopath model.

Predation mortality

The predation mortality shows little variation between the fish species and functional groups, with the predation mortality curves displayed in fig 3.16 being remarkably similar. Predation mortality peaked at around 0.01 g, then rapidly declined with size. The invertebrate functional groups, Crustacea, Annelida, Bivalvia and Gastropoda also had very similar predation mortality curves (fig 3.16), with predation mortality peaking at around 1g. These curves however are quite different from those of the fish species and functional groups; the initial slope is less steep with a small plateau before the peak at 1g, following the peak, predation mortality curves merge with those of the fish of equivalent size.

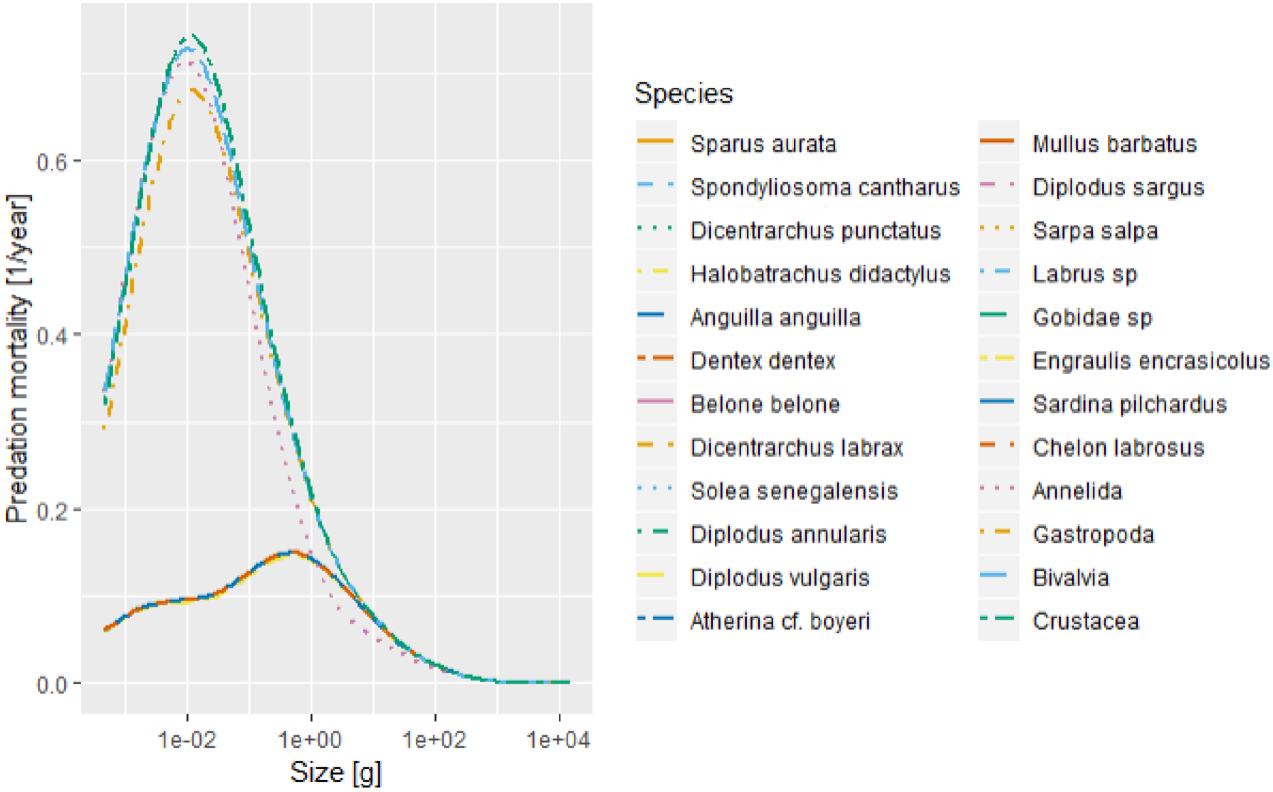

Figure 3.16. Predation rate as a function of size for the species/functional groups present in the size-spectrum model.

Mean predation mortalities for each species across all size classes were calculated from the MIZER estimates, which are presented with the Ecopath estimates. The size-spectrum model consistently estimated much lower predation mortalities compared with the Ecopath estimates (fig 3.17), with these differences being greatest for the invertebrate functional groups, peaking with Gastropoda.

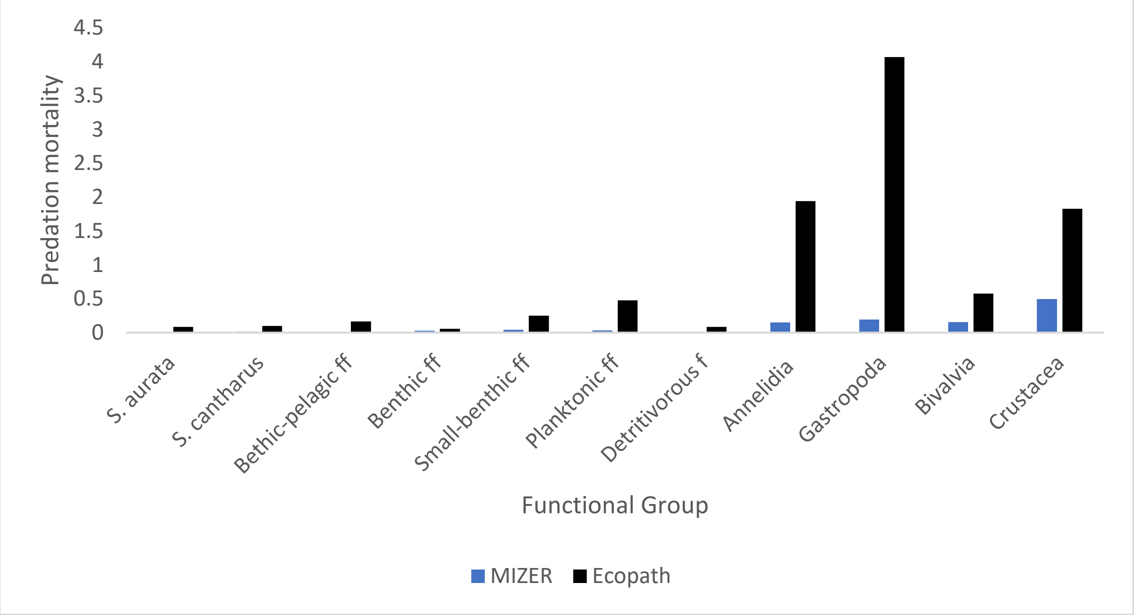

Figure 3.17. Bar chart showing the predation mortality estimates from Ecopath and the size-spectrum model for each functional group.

The sources of predation mortality for several representative species are shown in figure 3.18. Interestingly it appears that bivalves are the highest source of predation mortality for the fish species in the smallest size-classes, with this being replaced by *S. aurata* as the size of the prey species increases. *S. aurata* appears to cause the highest rates of predation mortality at around 1g, following this the predation mortality rate declines, with *H. didactylus* replacing *S. aurata* as the most voracious predator. The invertebrate functional groups had less dramatic changes in predation mortality with size, however Annelida and Gastropoda appeared to have a fairly linear decline with increasing size, however Crustacea predation mortality increased until peaking at around 0.01g. *S. aurata* and Gastropoda were the largest causes of predation mortality for the invertebrate groups.

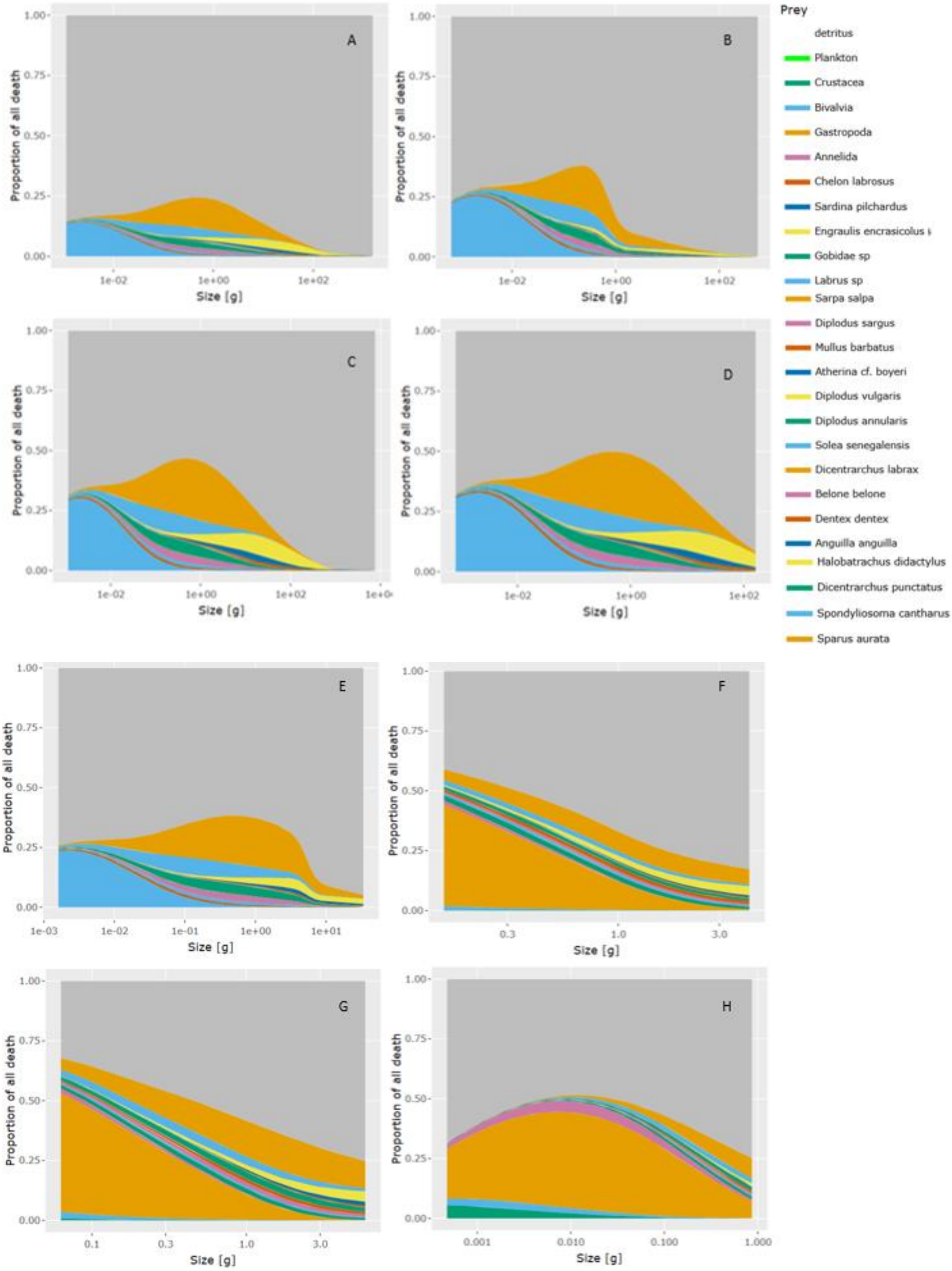A
B
C
D
E
F
G
H
Proportion of all death
0.00
0.25
0.50
0.75
1.00
Size [g]
1e-03
1e-02
1e-01
1e+00
1e+01
1e+02
0.001
0.010
0.100
1.000
0.1
0.3
1.0
3.0
Prey
detritus
Plankton
Crustacea
Bivalvia
Gastropoda
Annelida
Chelon labrosus
Sardina pilchardus
Engraulis encrasicolus
Gobidae sp
Labrus sp
Sarpa salpa
Diplodus sargus
Mullus barbatus
Atherina cf. boyeri
Diplodus vulgaris
Diplodus annularis
Solea senegalensis
Dicentrarchus labrax
Belone belone
Dentex dentex
Anguilla anguilla
Halobatrachus didactylus
Dicentrarchus punctatus
Spondyliosoma cantharus
Sparus aurata

Figure 3.18. Proportions of causes of total mortality with size for: A – S. aurata, B- S. cantharus, C- D. dentex, D – M. barbatus, E – S. pilchardus, F – Annelida, G – Bivalvia and H- Crustacea.

Chapter 4: Discussion

The size-spectrum model

The parameters presented in Table S1 (supplementary material) led to a balanced steady state, which appears to give a reasonable representation of the community in the Ria Formosa lagoon. This predicted the majority of the biomass to be concentrated in the smaller size classes, mostly due to the invertebrate functional groups. The feeding levels of many species appear to decline rapidly with age, with a corresponding decline in growth rates; this is thought to be due to declining abundance of prey as the individual grows and requires larger food items. This suggests that the community present in the Ria Formosa lagoon is food limited, possibly because the ecosystem is near its carrying capacity, as concluded by Gamito & Erzini (2005).

However, some issues remain regarding the size-spectrum; biomass accumulation is apparent in many species as can be seen by the fairly flat community-spectrum slope followed by a very rapid decline in biomass density with increasing size. Addition of size-dependent mortality improved this somewhat, as it acts to close the size-spectrum (Giacomini et al., 2016); however as these parameters were estimated, this causes a substantial increase in model uncertainty.

It is interesting that the feeding levels show a rapid decline with size, with corresponding declining growth rates with size. The Ria Formosa is considered an important nursery environment for many commercially important species (Vasconcelos et al., 2010), due to the high availability of food and low abundance of predators (Miller, 1985). The size-spectrum model produced appears to have reproduced these conditions to a certain extent, which can be seen by the high availability of small invertebrates (prey) and low biomass of large fish (predators). Many of the species that use the Ria Formosa as a nursery environment only reside there while in the small size-classes, then leave once they have grown sufficiently large (Vasconcelos et al., 2010). It is possible this decline in feeding level may represent one of the factors causing individuals to leave the security of the lagoon, a declining availability of preferential prey with increasing size.

Model parameterisation and calibration

Beta and sigma

The method of estimating the beta value based upon the mouth area to body length relationships presented by Karachle & Stergiou (2011), seemed to give reasonable estimates. Larger piscivorous predators such as *D. labrax* preferred larger prey, compared to the smaller invertebrate feeding fish, such as *S. cantharus*, preferring smaller prey, consistent with the diets reported on FishBase (2019). These seem reasonable considering that Rios et al. (2019), found increasing mouth area to body-length ratios corresponded with increasing piscivory. Furthermore, *H. didactylus* was predicted the second highest beta value; as *H. didactylus* are considered macrophagic carnivores, preferring a large prey items relative to their body size (Félix et al., 2016), this seems reasonable.

However, this method appeared to give unreliable estimates of prey size-selectivity for planktivorous fish; predicting *S. pilchardus* to prefer the largest relative prey size, with a beta value of 17. As *S. pilchardus* is known to feed upon very small plankton (FishBase, 2019), this beta value is clearly inaccurate.

Galván et al. (2010) compiled and reviewed 131 published trends and relationships between body size and $\delta^{15}N$ in inshore coastal fishes, finding that only 36% of these relationships were significant, with 60% non-significant, suggesting that non-size-selective feeding is in fact common. However, it must be noted that Galván et al. (2010) commented that few of the sample sizes were sufficiently large to adequately test slope significance, suggesting that this may be over-estimated.

Furthermore, Rios et al. (2019) reported a high variability in the relationships between mouth-size, size and body type with the trophic level of the fish, suggesting varying levels of size-dependent feeding. For example, the trophic level of Sparidae did not increase with increasing size (Rios et al., 2019), suggesting that their prey size may not increase with their body size.

The environment may influence these relationships, as reported by Layman, Winemiller, Arrington, & Jespen, (2005) investigating the body-size trophic-position relationship, for the fish community in a river in Venezuela. Although a tropical river is vastly different from the Ria Formosa lagoon system, there are some similarities in terms of the environment having a low stability, high biomasses of small size-classes, a large detrital component and the majority of prey species consisting primarily of algae/detritus-consuming invertebrates and small fish (Gamito et al., 2003; Layman et al., 2005). Layman et al. (2005) reported a significant correlation between predator and prey size, however there was no increase in trophic level, thus being considered a weak relationship, due to plasticity in prey-size-selection. This plasticity in the size-selection of predators was hypothesised to be advantageous, allowing predators to exploit a wider range of food sources, even if they would preferentially feed upon optimal sized prey. It is possible that this is the case in the study area.

Furthermore, whether or not the predator has teeth may have a large influence on the prey size selectivity; for example *S. aurata* is known to select large prey items and consume these by using their teeth to break them into edible portions (FishBase, 2019). This has been documented for the piscivore *Pomatomus saltatrix,* which was found to be not limited by gape-size due to their cutting teeth and select for large prey (Scharf et al., 2002).

Therefore, maximum prey size may not be limited by mouth area for all species present in the size-spectrum model, suggesting that they may select for larger or smaller prey than predicted by the relationship between body-length and mouth-area.

When data on Beta is not available, the mouth area to body length ratio can be used to estimate this parameter for many but not all species. This appears to be unsuitable for species such as planktonic filter feeders, or toothy predators where prey size is not limited by mouth size due to the ability to bite it into smaller pieces (Scharf et al., 2002). Furthermore, the environment and prey availability would likely further influence the predator-prey size relationships (Layman et al., 2005).

This high uncertainty regarding the beta and sigma estimates represents a major source of error in the size-spectrum model. As size-spectrum models consider growth and reproduction to be food-dependent (Scott et al., 2014), beta and sigma will likely have a major influence on these by dictating the availability of prey to a predator. This is supported by Thorpe et al., (2015), who concluded that after asymptotic length, the diet matrix and predator-prey size-selection parameters had the greatest influence on model output.

This questions the conclusion, that the water reservoir on the Ria Formosa lagoon is food limited. As this limitation may simply be a product of inaccurate beta and sigma values overly restricting the availability of prey. However, although this highlights parameter-based uncertainty, the similar conclusion of Gamito & Erzini (2005) that the lagoon is near the carrying capacity, suggests this conclusion is not entirely a product of parameter error.

Ks estimation

The default method of calculating Ks by: *Ks = h * 0.2* (Scott et al., 2013) proved ineffective possibly due to differences in the ratio of *h* to gamma (Scott et al., 2013), therefore estimates were obtained using resting oxygen consumption data from the FishBase oxygen table (Fishbase, 2019).

These estimates suffered from the same issue as the default method when incorporated into the model, the parameters create a feedback loop. The *h* parameter refers to the maximum food intake rate: in order to reach steady state this had to be increased sufficiently, with gamma, to allow that species enough food to grow to at least Wmat and allow some degree of reproduction, otherwise, the model would not reach steady state (Scott et al., 2014).

This resulted in the highest *h* values for species which have lower prey availability, as the lower abundance of prey requires higher *h* values to allow the predators to consume sufficient food, allowing growth and reproduction. As a positive linear regression between the *h* and Ks values estimated from O_2 consumption data was used to estimate Ks for species with no available O_2 consumption data, causing the species with the highest *h* to be predicted the highest Ks values. As the *h* values were highest for species with lower feeding levels, these had the highest Ks values. This resulted in the metabolic requirements being too high to cover due to lack of food, preventing the model from reaching steady state.

Estimating the Ks assuming that the individual has enough prey to grow to its Wmat resulted in more realistic predictions, with reduced pile up. Much care must be taken when estimating the Ks, as this interacts with several other parameters, which can lead to unrealistic predictions. Furthermore, the default method of estimating Ks proved unsuitable (Scott et al., 2013). The oxygen table from FishBase (2019) also has a high degree of variation between estimates. A study by Gillooly et al. (2001) also reported a high degree of variation between O_2 consumption when compiling a data base of published estimates for a variety of species. Therefore, estimates of Ks based upon O_2

consumption data should be treated with caution, as inaccuracies in the estimates may have a dramatic effect on the output of the model. These Ks estimates are a major source of uncertainty in this size-spectrum model.

Additional size-dependent mortality

The model parameters without the additional size-dependent mortality predicted lower growth rates in many cases, however these differences were not extreme. This is likely due to the food availability and feeding levels being almost identical, causing similar growth rates and W_∞. The lack of mortality in the larger sizes can lead to biomass accumulation, when biomass of a certain species accumulates in large size-classes, which leads to depletion of prey in their preferred prey size-class (Guiet et al., 2016a). As growth in size-spectrum models is food dependent, this can limit growth, preventing the individual from outgrowing that particular size-class (Scott et al., 2013).

Care must be taken when basing the parameters of a size-spectrum model on those estimated from non-size structured models; these differences suggest that parameters leading to a balanced-state in Ecopath may not necessarily lead to a realistic steady-state size-spectrum.

The assumption that the net prevented immigration/emigration, fishing and bird predation in Gamito & Erzini (2005) is a good example of this; as these led to steady state in MIZER with a lower overall abundance but larger mean-size of fish compared to what was observed in the data. This is possibly because the balanced-state predicted by the Gamito & Erzini (2005) model and the steady-state predicted by the size-spectrum model in (fig 3.1), was that immediately before the isolation of the lagoon, as impacts of immigration/emigration, bird predation and fishing are still apparent in the size-structure of the sampled individuals.

This highlights a short-coming of static models such as Ecopath, as these do not consider time and the associated changes that isolation will have on the lagoon community (Christensen et al., 2000).

Comparisons

Growth

The von Bertalanffy parameters W_∞ and K(vb) for *S. aurata, S. cantharus* and *D. vulgaris* were estimated from the data of Gamito & Erzini (2005), the predicted size-at-age-data from MIZER and from Ecopath, allowing comparison with the predicted growth rates from both models.

Ecopath predicted the lowest W_∞ estimates; with the size-spectrum model predicting W_∞ the second lowest values for *S. cantharus* and *D. vulgaris*. However, the size-spectrum model estimate for *S. aurata* was higher than both the data and FishBase (2019) estimates. It is interesting the Ecopath predicted such a low W_∞ for *S. aurata* (157.3g), when FishBase (2019) estimates Wmat to be 297g. If this was the size-spectrum model, this would not lead to a steady state, as *S. aurata* would be unable to reproduce due to being unable to grow to maturity (Scott et al., 2013).

There are several explanations for the difference between the W_∞ predicted from the data and the estimates from MIZER and FishBase. The stomach content analysis study by Gamito et al., (2003) used the same study site and data as Gamito & Erzini (2005), meaning that a portion of the individuals sampled were sacrificed for stomach content analysis. For *S. aurata* a vast proportion of the large individuals were killed for this purpose, effectively eliminating that cohort. This loss of the larger individuals would lead to a lower predicted W_∞. Furthermore, cohort analysis is most effective when multiple cohorts can be identified and using only a single cohort to estimate growth rates is unreliable (Pauly & Morgan, 1987).

The size-spectrum model data led to lower W_∞ estimates than the data and FishBase for *S. cantharus* and *D. vulgaris;* a possible explanation for this is that MIZER predicts a lower W_∞ due to declining prey abundances as they reach larger sizes, indicated by the declining feeding level with size for these species.

The proportion of detritus in the diet increased with age; as the availability of detritus stays the same regardless of predator size, as it is considered a none-size structured resource (Blanchard et al., 2009; Scott et al., 2013), therefore an increase in the proportion of detritus in the diet suggests a decline in the availability of other prey groups. It seems unlikely that in reality the proportion of detritus consumed increases with a predator size; furthermore, this is in conflict with the Gamito et al. (2003) stomach content study. Therefore, it seems likely that this phenomenun represents an inaccuate allometric scaling relationship between detritus encounter and consumption.

It is surprising that the estimate from the predicted data from the size-spectrum model for the W_∞ of *S. aurata* is higher than both the data and the FishBase estimate, considering these also suffer from declining feeding level with increasing size.

MIZER predicted a much lower K(vb) than the data or input for *S. aurata*, this is likely due to the larger W_∞ as larger asymptotic weight generally means lower K(vb) values. However, the predicted K(vb) for *S. cantharus* from MIZER was the same as the Ecopath and FishBase estimates. However, the estimate for *D. vulgaris* from MIZER was lower than the estimate from FishBase and much lower than the estimate from Ecopath.

Diet proportions

A diet matrix was constructed by Gamito & Erzini (2005) based upon the stomach content data from Gamito et al. (2003). This is a static diet matrix and does not consider the availability of prey, seasonal changes in biomass or the size of the prey item relative to the size of the predator (Christensen et al., 2000). However, this still provides reliable diet composition estimates; especially considering the stomach content analysis was performed in the study area, therefore relative prey abundances at that specific time would likely be reflected in the stomach content data.

Overall the diets predicted by the size-spectrum model were similar to the Ecopath estimates and findings of Gamito et al., (2003); with the only major difference being the size-spectrum methodology predicting plankton to make up a large proportion of the diet of many species, which do not feed upon plankton in the Ecopath model.

This difference is likely due to the fact that Gamito et al., (2003) sampled mostly adult specimens of these species, which would not be feeding heavily on plankton at this stage in their lives. Many species including large predators undergo dramatic shift in diet composition as they develop from the planktonic stage to maturity (Wells et al., 2008), rendering this diet matrix representative of adults of these species only. Furthermore, small plankton can be difficult to quantify in stomach contents analysis, as their small-size and fragile nature means they are quickly digested and difficult to identify (de la Morinière, 2003), therefore this component may have been under-represented.

The diet composition estimated by MIZER at the species Wmat showed more similar diet proportion estimates to Gamito et al., (2003), however plankton still represented a significant proportion of the diet. This is surprising as this was still the case for groups of species with high Wmat and beta values, such as benthic-pelagic feeding fish. A possible cause may be that plankton have such a high biomass and abundance compared to the other components, meaning that even if the majority of interactions do not result in predation, the high number of these may still result in a large contribution to the diet. This shows that care must be taken when producing the predation interaction matrix, in order to avoid the obvious inaccuracy of adult fish having an excessive proportion of plankton in their diets.

The size-spectrum model predicted a higher consumption of Annelida than the Ecopath model, both overall and at Wmat, due to the interaction with Annelida being left high in the interaction matrix. This was because many species were already becoming food limited with increasing size and the parameters were not leading to a realistic steady state, therefore interaction with Annelida was increased to allow access to more prey. As prey abundance has a significant effect on the diet composition in size-spectrum models (Scott et al., 2013), it is unsurprising the Annelida make up the largest proportion of the diet of many species, as they have the largest biomass.

It is also possible that Annelida component of the diet was underrepresented by Gamito et al. (2003), as Annelida are often very soft, small, fragile and easily digested, making their contribution difficult to quantify in stomach content analysis (Stergiou & Karpouzi 2002; Gamito et al., 2003). Therefore, a higher proportion of Annelida in the diet of the species in the size-spectrum model may not be an inaccurate assumption.

The size-spectrum model predicts a size-dependent ontogenetic shift from a plankton dominated diet, to one comprised mostly of the invertebrate groups with an increasing proportion of fish species in the largest sizes, which has been documented for many species (Stoner & Livingston, 1984; Wells et al., 2008). Species with lower W_∞ and higher beta values generally had a larger proportion of plankton and invertebrates and a lower proportion of fish in their diet than the larger species with low beta values, as they select for smaller prey.

MIZER assumes a homogeneously mixed population with predatory interactions primarily determined by the abundance and the size of the prey items (Scott et al., 2013). This approach is simpler and requires less data and parameterisation; however this is achieved through reliance on generalised size-based relationships (Jacobsen et al., 2015). Greater resolution of prey preference independent of size can be included by careful use of the interaction matrix, although this is accompanied by increased data requirements (Essington, 2007).

The interaction matrix and feeding parameters of the size-spectrum model (Tables S1 and S2) predicted similar results to the Ecopath diet matrix, based upon the findings of Gamito et al., (2003), suggesting these predicted a relatively accurate diet. A wide variety of prey was found in the diets of the species studied by Gamito et al. (2003), which was hypothesised to provide an advantage in environments of low stability and poor diversity. This suggests that 'everything eats everything' method of estimating the diet composition may be suitable for predicting diet composition in communities with low levels of specialised feeding. However, for environments with high stability and species with highly specific diets, care should be taken in construction of the interaction matrix in order to properly represent these processes (Essington, 2007).

Consumption/Biomass

Estimates of Q/B for the individual size-classes gave a wide range of values. This is similar to the growth rates with these often displaying the fastest growth rate in the early life stages (Casselman, 1990). This seems reasonable considering that the size-spectrum models calculate growth as a proportion of the individuals consumption, once the metabolic resting requirements have been met (Scott et al., 2013). Therefore, it is unsurprising that MIZER predicted the highest Q/B estimates when the growth rates are highest, in the smallest size-classes (Casselman, 1990).

The original comparison of the total consumption/total biomass predicted by the two methodologies revealed extremely large discrepancies between the estimates. Some species or functional groups appeared to have very similar estimates, such as *S. aurata* and *S. cantharus*, whereas other groups had estimates which were completely unfeasible, such as Benthic-pelagic feeding fish which had a Q/B estimate of 2227.76.

The size-spectrum model uses a multi-species frame-work, with almost all species present explicitly modelled, due to the low biomass and abundance of fish in the study ecosystem, many of these could be considered background species, with low abundance and biomass. Size-spectrum modelling methodologies can struggle to reach steady state if there are many background species present (Scott et al., 2013); which is also the case in other modelling methodologies such as Ecopath (Christensen et al., 2000; Ainsworth & Walters, 2015).

The benthic-pelagic feeding fish functional group has a low biomass and abundance, comprised mostly background species, which is likely the cause of these unfeasible estimates. The species level Q/B estimates used to obtain the estimates for the functional groups supports this, with *D. labrax*, which has the lowest biomass, having the highest Q/B estimate of 12166.39.

This is an unsurprising result as considering that both Blanchard et al., (2014) and Szuwalski et al., (2017) modelled only 12 species/groups in multi-species size-spectrum models of the North Sea and East China Sea, respectively, therefore the 24 species and groups included in this size-spectrum model was certainly overly ambitious.

The corrected estimates resulted in estimates within the expected range, with Ecopath predicting consistently higher estimates. Part of this discrepancy may be due to Ecopath predicting higher predation mortalities for these groups predicted by Ecopath, as Palomares & Pauly, (1998) found that increasing mortality-rates had a positive effect on Q/B ratios.

Furthermore, the parameters beta & sigma may render portions of the prey species populations invulnerable to predation, as no individuals are selecting for individuals in those particular size-classes. As Ecopath does not consider size in prey selection (Christensen et al., 2000), all the population of a prey species are considered equally vulnerable to predation, potentially allowing for greater prey availability resulting in greater consumption. This is supported by the much lower predation mortality rates predicted by the size-spectrum model.

Production/Biomass

The Ecopath model predicted higher P/B ratios for all species and functional groups except for *S. aurata*. This is likely due to the lower consumption/biomass ratios predicted from the size-spectrum model; as production in size-spectrum modelling is consumption dependent (Scott et al, 2013). Therefore, this likely again caused by beta and sigma limiting the amount of prey available.

Predation mortality

The size-spectrum model predicted remarkably similar predation mortality curves for fish species and functional groups. The invertebrate groups also show similar growth curves; however, the predation mortality peaks at 1g compared with 0.01g for the fish species/functional groups. This similarity in predation is due to the interaction matrix being set at 1 for all fish species, meaning the predation rates will be the same for each size category, due to being determined by size (Scott et al., 2013).

The predation mortality rates are lower for the invertebrate groups; however, they do not have such dramatic increases and decreases, which results in these having an overall higher predation mortality. A possible reason for this is that due to their small size, they do not grow sufficiently to be able to avoid predation from smaller predators, which has been documented in many fish species (Sogard, 1997). Another possible reason for the high mortality of fish in the small size classes is because of predation from bivalves, as these were a significant source of mortality for the early life stages, however this source of predation drops rapidly with size. Ecopath does not include these size-dependent predatory interactions, except when the multi-stanza function is used, which greatly increase data requirements (Christensen et al., 2000).

Inclusion of size-dependent predatory interactions is important as mortality in the early life stages can often have a large impact on recruitment (Anderson, 1988); whist also being hard to quantify, possibly leading to increased uncertainty regarding predictions (Tsou & Collie, 2001).

Overall estimates of predation mortality were obtained from both models. Ecopath generally predicted higher predation mortalities for all species, however this was most extreme for planktonic fish, Annelida, Gastropoda and Crustacea. This is possibly due to Ecopath predicting consumption independent of the abundance and size of the available prey, assuming that the predator species is able to feed upon all prey items; whereas in the size-spectrum model only individuals in the size selection range of the predator will be vulnerable to predation. This may be the cause of the lower predation mortalities. It is interesting that the size-spectrum model predicts such low predation mortalities, when many species appear to have stunted growth rates due to declining feeding levels with size.

This highlights an important difference between the model workings, as in Ecopath prey availability is determined by the biomasses present (not considering the interaction matrix) (Christensen et al., 2000), whereas the size-spectrum model uses this and also the size-structure of the prey population. This suggests that in size-spectrum models predicts only a portion of a species to be vulnerable to predation at any one time, whereas Ecopath considers all to be equally vulnerable.

Chapter 5: Conclusion

A multi-species size-spectrum model was constructed and calibrated to the data set of Gamito & Erzini (2005), reaching steady-state. This produced a wide range of results with some estimates very similar to the Gamito & Erzini (2005) Ecopath model, although some had very large differences, with some of the estimates taken from the size-spectrum model being totally unfeasible. It is probable that the high number of species and groups included in the size-spectrum model, many of which have very low abundances and biomass, were a major cause of these unrealistic estimates.

The corrected estimates did not appear to be influenced by the abundance densities and were considered reliable; the Ecopath model predicted generally higher estimates of Q/B, P/B and predation mortality. This was thought to be due to the predation kernels rendering portions of the prey population unavailable as prey (due to the size), resulting in lowers predation mortality consumption/biomass. As in size-spectrum modelling production is consumption dependent (Scott et al., 2013), this offers and explanation for the lower predicted P/B ratios.

Parameter estimation and calibration proved difficult as no data was available on beta, sigma, and Ks; therefore these had to be estimated using new methods of extracting parameters from existing data sets, leading to a higher degree of parameter-based uncertainty. Furthermore Thorpe et al. (2015) found that behind W_∞, the interaction matrix, beta and sigma had the greatest contribution to parameter-based uncertainty, due to growth being food-dependent. This surrounds the conclusion that many species in the size-spectrum model are food limiting with uncertainty, as this limitation may be due to overly restrictive feeding parameters. However, as Gamito & Erzini (2005) reached the same conclusion, this is likely accurate.

Additional size-dependent mortality was added to the model because the low mortality rates in the large size-classes due to no fishing and low predation mortality due to lack of large predators led to biomass accumulation and pile up in the larger size classes. This suggests that because a certain parameter set leads to a balanced state in Ecopath, does not necessarily mean that these will reproduce an accurate prediction in a size-spectrum model.

A major difference between the two models is that Gamito & Erzini (2005) concluded that Ria Formosa lagoon is mostly detritus-driven ecosystem, however the size-spectrum model predicts much higher consumption of plankton. If plankton is reduced and detritus is increased, it leads to the unrealistic scenario of large adult predators feeding almost entirely on detritus, as this is modelled as a non-size-structured component (Scott et al., 2013). This suggests that size-spectrum is more suited to modelling plankton-driven systems, even if detritus can be included.

The predicted diet composition was similar to that reported by Gamito et al., (2003); aside from the significant proportions of plankton present in many species diets, suggesting that the feeding parameters used in the size-spectrum model effectively reproduced the diets of the species present in the study area.

The growth of many species present, especially the large predators, appears to be limited by decreasing prey availability (declining feeding level). The size-spectrum model generally predicted growth rates lower than those estimate from FishBase (2019) or the data, with *S. aurata* being an exception assumed to be due to the loss of the larger individuals for stomach content analysis, influencing the growth predictions.

MIZER is a recently developed open access size-spectrum modelling software designed to be user friendly and allow scientists easy access to size-spectrum methodologies (Scott et al., 2014). Issues regarding inclusion of too many background species are thought to be the cause of the improbable estimates. Parameter estimation and calibration of the model proved difficult and likely increased parameter-based uncertainty significantly. This highlights the need for better methodologies for estimating these and the improving the calibration process; this will likely improve widespread uptake of the MIZER and size-spectrum modelling methodologies.

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Supplementary materials

Supplementary materials are supplied electronically.