UNIVERSIDADE DO ALGARVE
FACULDADE DE CIÊNCIAS E TECNOLOGIA

THE IMPACT OF JELLYFISH ON THE ESTUARINE ECOSYSTEMS: THE GUADIANA STUDY CASE

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Dissertation of Master thesis by
Erasmus Mundus Master of Science on Ecohydrology

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2013

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Scientific area: Marine Ecology/ Coastal Ecohydrology

Key words: newly introduced species, *Blackforida virginica*, modeling, food web dynamics, flow changes, zooplankton, ichthyoplankton

Palavras-chave: espécies invasoras, *Blackforida virginica*, modelação, dinâmica da teia trofica, alterações de caudal, zooplâncton, ictioplâncton

Date: 13th of December 2013

Title of dissertation: The impact of jellyfish on the estuarine ecosystems: the Guadiana study case

To Lana,

my newly born sweetheart,

who has been literally breading with me through this master thesis.

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Abstract

The presence of newly introduced species of jellyfish in the estuarine systems can result in diverse disruptions at different levels of the food web affecting native competitor species, predators and prey. Newly introduced species of jellyfish can poses a threat to this system by affecting the well- established food web dynamics. There was a noticeable increase in jellyfish presence in years after the Alqueva dam in relation to the species *Aurelia aurita*, *Blackfordia virginica*, *Maeotias marginata* and *Catostylus tagi*. *B. virginica* has become the most widely spread species within the Guadiana Estuary. Its presence might be an important factor influencing the pelagic ecosystem in Guadiana by predation effect and competition with other predators. As zooplankton presents a main food source for zooplanktivorous fish and fish larvae the jellyfish species may be able to over compete the native fish population or decrease the food supply to insufficient level. This could directly result in decrease of zooplankton abundance correlated to an increase of phytoplankton and consequently in eutrophication. Presumably there is a potential for jellyfish species annual growth and establishment. This work presents a food web model located in the Guadiana Estuary situated between South of Spain and Portugal where the impact of jellyfish *B. virginica* was evaluated in a model based on the variation of biomass of each state variable (mgC m-3). *B. virginica* has been present in the estuary since 2002 with the highest abundance of 31.2 ind. m-3 measured in 2008. The Guadiana Estuary had experience significant changes related to fresh water availability as Alqueva dam was built in 2002. What impact does water discharge and pattern of precipitation rate related to NAO has on present ecosystem has been evaluated through the nutrient and seston concentration in the model. Extential sampling data from year 1997 up to 2012 was conducted in Guadiana Estuary which data were used through the process of statistical analysis for the model functioning. Guadiana Estuary is divided into three sub-areas: upper with stations Alcotium and Gueirros do Rio; middle with sampling at Almada de Ouro and Foz de Odeleite; and lower estuary where samples were taken at Esteiro Carrasqueira, Barra, River Plume (Pluma) and Praia de St. Antonio station.

Presence of *B. virginica* normally takes place in brackish zone where ETM zone is present which is characterized by mixed salinity. We have developed a seasonal food-web model based on the annual presence of jellyfish *B. virginica*, which is from beginning of June to the end of August. We have used 6 groups of marine organisms represented as state variables in the model. Groups of phytoplankton, zooplankton, ichthyoplankton (fish eggs and fish larvae separated), *B. virginica*, juvenile European anchovy (*Engraulis encrasicolus*) and their biomass, distribution, and diet were used from survey data. Food web model was created within the most important groups in the ecosystem and presented in the conceptual diagram. For our theoretical network model we have worked on a predator- prey relation expressed with the Michaelis- Menten exponential response. Through different sensitivity tests we have shown the potential impact of jellyfish species on the present food web through different scenarios. Statistical analysis based on average abundance rate of *B. virginica* and zooplankton compared to abiotic conditions was done for an easier clarification and comparison with the results from the model. The results obtained by the model developed in this thesis are in conformity with field measurements to what it concerns biomass values of each individual group in the model. The model shows a significant impact of *B. virginica* over all groups of species presented in the model. Nutrient and seston concentration appears to be the most influential trigger for the majority of the food web dynamics. Sensitivity analysis has proven that the phytoplankton, zooplankton and juvenile anchovy are the most sensitive organisms in the whole food web influenced by nutrient availability and water discharge. *B. virginica*, fish eggs and fish larvae biomass has proven to vary upon these conditions tested in different runs though they are not affected directly. There is significantly high jellyfish biomass increase in case of high nutrient concentrations. In similar situation if *B. virginica* is not present there is a high rise in ichthyoplankton biomass, juvenile anchovy and zooplankton. Situation with low water discharge and high nutrient amount appears to be the most devastating for the estuarine ecosystem. In situation with low nutrient conditions the phytoplankton, fish eggs, fish larvae and *B. virginica* biomass increases through summer but zooplankton and juvenile anchovy

biomass decreases. Trend of this groups tend to change in different nutrient conditions. Significant changes in biomass content are noticed between all groups. Compared to low nutrient concentration simulations in high nutrient concentration present that all state variables have an initial increase and only due to the predatory effect the decrease of certain groups occur. Detritus production trend follows up the movement of biomass increase and decrease. There is a strong correlation of *B. virginica* increase due to predational effect over zooplankton which levels seem to be detrimental for the fish eggs. Fish larvae group appears to be the most resistant group for the *B. virginica* pressures on the ecosystem. By the results in the model we can see that the NAO index can reflect a pattern of each individual biomass group in the food web as it is partially responsible for the nutrient concentration in the estuary. The most impacted group by *B. virginica* is zooplankton which controls phytoplankton growth from top down. These relation causes bottom up control as zooplankton biomass influences the ichthyoplankton and juvenile anchovy biomass. In case of high winter water discharge the detritus production is higher and the turbidity at the mouth of the estuary attracts higher amount of adult's fish to spawn. Higher fish eggs biomass causes higher and faster growth of *B. virginica* which is able to consume higher amount of zooplankton and with that controls the decrease in juvenile anchovy population and fish larvae survival rate. Possible presented scenario is over- predation of zooplankton which can lead to phytoplankton bloom.

Resumo

A presença de espécies de medusas recentemente introduzidas nos sistemas estuarinos pode resultar em diversas rupturas nos diferentes níveis da teia alimentar afetando espécies nativas competidoras, predadores e presas. Espécies recentemente introduzidas de representam uma ameaça para este sistema, afetando a dinâmica da rede trofica. Houve um registo de frequência medusasapós a construção da barragem do Alqueva, de especeis de organismos gelatinosos, como e *Aurelia aurita*, *Blackfordia virginica*, *Maeotias marginata* e *Catostylus tagi*. Em terminadas alturas, *B. virginica* tornou-se a

espécie mais representada dentro do Guadiana Estuário. A aua presença pode ser um fator importante que influencia o ecossistema pelágico no Guadiana através do potencial de predação e competição com outros predadores. Como zooplâncton apresenta a principal fonte alimentar para larvas de peixe e peixe zooplanktivorous, estas espécies podem ser capazes de competir com a população de peixes nativos ou diminuir a oferta de recursos pesqueirospara o nível insuficiente. Outra consequencia seria a redução de zooplâncton e um consequente um aumento de fitoplâncton e, provavel, na eutrofização. Este trabalho apresenta um modelo de teia alimentar para o Estuário do Guadiana situado entre o Sul de Espanha e Portugal, onde o impacto da medusa *B. virginica* foi avaliada com base na variação da biomassa de cada variável de estado (mgC m-3). *B. virginica* esteve presente no estuário desde 2002, com a maior abundância de 31. 2 ind. m-3 medido em 2008. O Guadiana Estuário sofreu mudanças significativas em relação à disponibilidade de água doce em aprticular após a construção da barragem doAlqueva em 2002. Qual o impacto que descarga de água e padrão de taxa de precipitação relacionada com NAO tem no presente ecossistema tem sido avaliada através da concentração de nutrientes e seston no modelo. Dados de amostragem desenvolvidas de 1997 até 2012, no Estuário do Guadiana foram utilizados durante o processo de análise estatística sobre o funcionamento do modelo de. Guadiana Estuário está dividido em três sub-áreas : superior, com estações Alcotium e Guerreiros do Rio ; medio com estaçoes em Almada de Ouro e Foz de Odeleite , e inferior com estações no Esteiro Carrasqueira , Barra , Pluma e Praia de St. Antonio. A presença de *B. virginica* normalmente ocorre na zona salobra zona onde a ETM estiver presente, e caracteriza-s por uma zona de mistura de salinidade. Desenvolveu-ses um modelo sazonal –de teia trofica com base na presença anual de *B. virginica* , entre o início de junho até final de agosto. Usaram-se 6 grupos de organismos marinhos representados como variáveis de estado do modelo:fitoplâncton, zooplâncton, ictioplâncton (ovos e larvas de peixes peixe separados), *B. virginica*, juvenil de anchova europeia (*Engraulis encrasicolus*) e sua biomassa, a distribuição e dieta foram utilizados a partir de dados de pesquisa. O Modelo da teia trofica foi criado dentro dos grupos mais importantes no ecossistema e apresentados no diagrama conceitual. Para o nosso modelo de rede teórica trabalhou-se numa relação predador-presa expressa com a resposta exponencial Michaelis -Menten. Através de diferentes testes de sensibilidade que têm demonstrado o impacto potencial das espécies de medusa na presente teia alimentar através de diferentes cenários. A análise estatística das taxas abundância média de *B. virginica* e zooplâncton e em comparação com as condições abióticas foi feito para uma validaçãoe comparação com os resultados do modelo.Os resultados obtidos pelo modelo desenvolvido nesta tese estão em conformidade com as medições de campo para o que diz respeito a valores de biomassa de cada grupo individual no modelo. O modelo mostra um impacto significativo de *B. virginica* sobre todos os grupos de espécies incluidas na analise. A concentração de nutrientes e séston parece despoletar a dinâmica da teia alimentar. A análise de sensibilidade mostrou que o fitoplâncton , zooplâncton e anchova juvenil são os organismos mais sensíveis em toda a teia alimentar influenciada pela disponibilidade de nutrientes e descarga de água doce. *B. virginica,* ovos de peixe e biomassa de larvas de peixes provou variar de acordo com estas condições testadas em testes diferentes, embora eles não sejam afetados diretamente. Não é significativamente elevado aumento da biomassa medusas em caso de altas concentrações de nutrientes. Em situação semelhante se a *B. virginica* não está presente há um elevado aumento na biomassa ictioplâncton, anchova juvenil e zooplâncton. Em situação de baixa descarga de água docee elevada quantidade de nutrientes parece ser a mais devastadora para o ecossistema estuarino. Em situação com baixas condições de nutrientes, de fitoplâncton, ovos e larvas de peixes, a biomassa *B. virginica* aumenta ao longo verão, mas o zooplâncton e a biomassa juvenil de anchova diminuiu. A importância destes grupos tende a mudar em diferentes condições nutricionais. As mudanças significativas no teor de biomassa são notorios entre todos os grupos. A comparação com as simulações de concentração de nutrientes baixos a alta concentração de nutrientes presentes provoca em todas as variáveis de estado um aumento inicial e só devido ao efeito predatório a diminuição de certos grupos ocorre. A tendência de produção de detritos acompanha o movimento de aumento da biomassa e sua redução. Há uma forte correlação entre aumento *B. virginica* devido ao efeito predatório sobre o zooplâncton que os níveis parecem ser prejudicial para os ovos de peixe. O grupo larvas de peixes parece ser o grupo mais resistente para as pressões *B. virginica* sobre o ecossistema. Pelos resultados do modelo, podemos ver que o índice NAO pode indicar um padrão da biomassa individual na teia trofica, uma vez que é parcialmente responsável pela concentração de nutrientes no estuário. O grupo mais afetado por *B. virginica* é zooplâncton que controla o crescimento do fitoplâncton , de cima para baixo. Esta relação causa um controle pela basepois a biomassa de zooplâncton influencia o ictioplâncton e biomassa juvenil anchova. Em caso de de alta descarga de água doce no inverno a produção de detritos é maior e a turbidez na foz do estuário atrai maior quantidade de adultos para desovar e para a pesca. Maior biomassa de ovos de peixe provoca um crescimento maior e mais rápido de *B. virginica* que é capaz de consumir maior quantidade de zooplâncton e com que controla o decréscimo na população de anchova juvenil e taxa de sobrevivência de larvas de peixes. Como conclusão pode-se referir que os resultados obtidos com o modelo desenvolvido nesta tese estão em conformidade com as medições realizadas in situ no que se refere aos valores de biomassa de cada grupo individual. Para além disso é um dos poucos estudos existentes a nível da etia trófica, onde as medusas são incluidas como grupo individual.

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Introduction

The productive coastal areas of the oceans have been recognized as belonging to the most valuable ecosystems on Earth, from an ecological and socio-economic point of view (Costanza *et al*., 1997); yet, they are also among the most endangered due to a variety of direct and indirect anthropogenic disturbances such as pollution, marine and coastal construction, maritime transport, overfishing, invasive species, and climate change (Halpern *et al*., 2008, Nastav *et al*., 2013). The estuaries present a very powerful connection between the inland waters and marine environment and with its specificness they are one of the most productive and fragile ecosystems (NOAA, 2012). Anthropogenic modification of natural river pathways has been largely practiced in Spain (Alonso-Franco, 2003). Guadiana Estuary is no exception regarding increased anthropogenic modifications. River regulation has normally a negative impact on the ecosystem. Dams constitute obstacles for longitudinal exchanges along fluvial systems and so result in “discontinuities” in the river continuum (Ward et al., 1995). Building of the Alqueva dam on Guadiana River, the largest dam structure in Europe, has definitely caused certain amount of modifications on the local natural environment, specifically on the downstream estuarine and adjacent coastal ecosystems. Its floodgates were closed on February 8th 2002. Since then, river flow regulation increased from 75% to 81% (Rocha *et al*., 2002; Morais *et al*., 2009). Previous research have found increased modifications within the ecosystem (Rocha et al., 2002, Chicharo et al., 2009b, Morais et al., 2009, Muha et al., 2012) after the closure of the dam. To what extent ecosystem is being modified by variations in water discharge in the Guadiana Estuary Wolanski et al. (2006) presented in an ecohydrological model. With barriers on the river there is a consequential increase in water temperature which can provide potential new living places for the alien species that were limited before to the more equatorial waters. The newly introduced species particularly Cnidarians, jellyfishes are potential new colonizers of coastal environments with a great level of success at becoming a dominated organism in non-native ecosystem. The seasonal jellyfish bloom is common in many marine environments, but there is also great interannual variability (Purcell, 2005; Primo, 2012). In the

Guadiana jellyfish species are increasing annually as it comes to its biomass or species presence. The new introduction of the jellyfish species in the Guadiana is interestingly overlapping with the year of closure of the Alqueva dam. There was a noticeable increase in jellyfish presence in years after the Alqueva dam in relation to the species *Aurelia aurita, Blackfordia virginica*, *Maeotias marginata* and *Catostylus tagi*. *B. virginica* has become the most widely spread species within the Guadiana Estuary. Its presence might be an important factor influencing the pelagic ecosystem in Guadiana by predation effect and competition with other predators. Presumably there is a potential for jellyfish species annual growth and establishment.

Blackfordia virginica Majer (Fig. 1), 1910 is a well-known invasive medusa inhabiting estuarine areas (Chicharo *et al*., 2009b). These hydromedusae, native to the Black Sea, are becoming a prominent feature of many estuarine communities (Mills, 2001). They have been established in estuarine areas around the entire world (Chicharo *et al*., 2009b). Yet, surprisingly little is known about their biological requirements, habitat use, and potential impacts where they have been introduced (Schroeter, 2008). Their appearance was previously investigated in Suisun Marsh in the upper San Francisco Estuary (Schroeter, 2008, Mills et al., 1995, 2000), Napa and Petaluma Rivers (Wintzer et al., 2013) and Baltic Sea (Väinölä et al., 2013). They are identified as euryhaline species (Mills et al., 1995). *B. virginica* medusae are transparent, unpigmented, and delicate, with up to 80 very fine tentacles at maturity (Mills et al., 1995). *B. virginica* does not possess obvious light-sensing organs, but may still be responding to light-dark cues, as most gelatinous species are believed to have evolved some form of photoreception (Anderson, 1985, Wintzer et al., 2013).

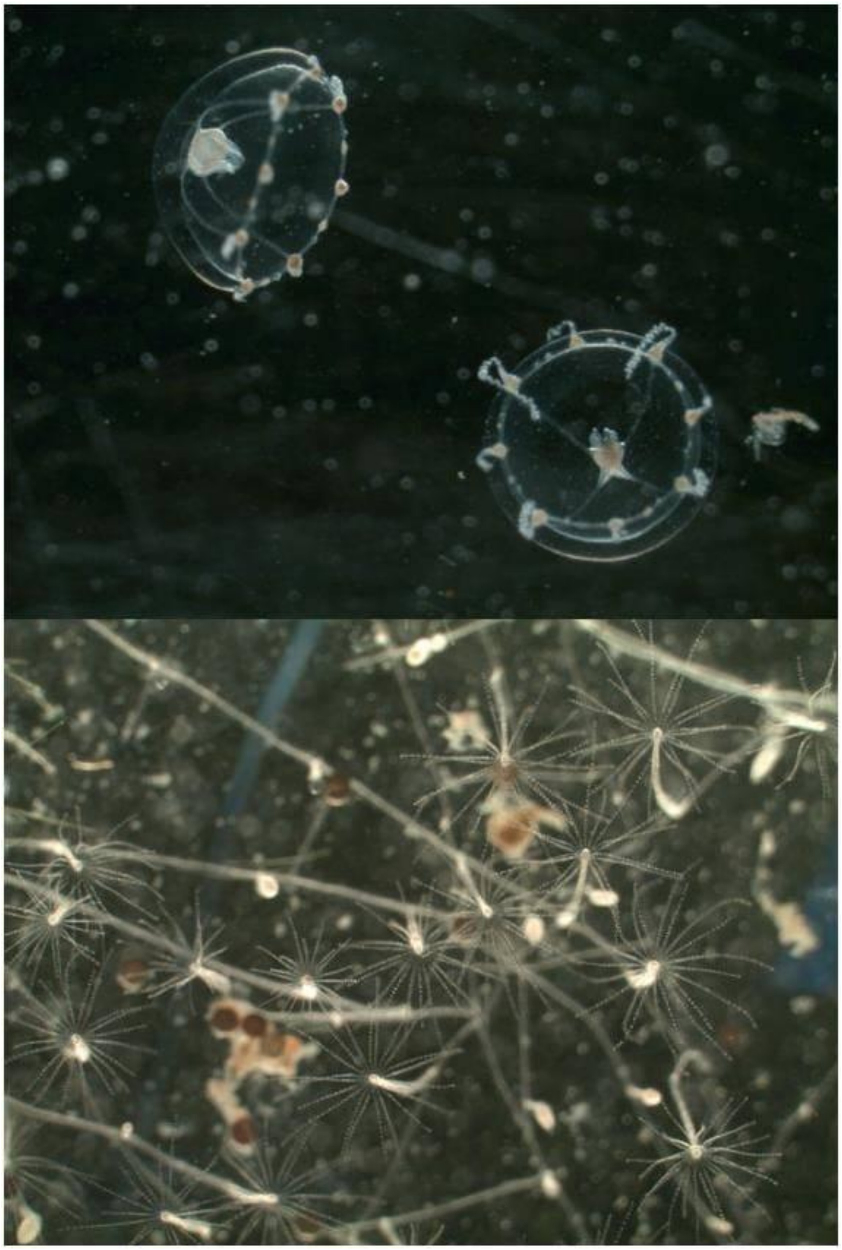

Figure 1-Upper part- juvenile pelagic *Blackfordia virginica*; lower part-polyps of some species, hydroid stage;

http://invasions.si.edu/nemesis/browseDB/SpeciesSummary.jsp?TSN=49780**.**

The *B. virginica* was observed in the Guadiana for the first time in July 2008, at the transitional zone of the estuary (brackish area) by (Chicharo et al, 2009b). High densities of medusae (> 100.100 ind. m-3) were collected in most samples from the Middle estuary, with a maximum 3170.1 ind. 100 m-3 in (Posto Cinturão, geographic coordinates 37º15'30"N, 7º25'58"W). Specimens of both sexes were found, over a wide range of sizes (6-19 mm) and maturation stages and in such large numbers that would suggest local reproduction (Chicharo et al., 2009b). A minimum bloom initiation temperature of approximately 19 °C was assumed for release of medusae from polyps, when salinities are also suitable (Schroeter, 2008). Though there is an average biomass increase of *B. virginica* in Guadiana no polyps have been found yet. New studies revealed that the species was present already before in year 2002 and not in July 2008 as presented at the research (Chicharo *et al*., 2009b). There is no published information about the effects of *B. virginica* on surrounding macrofauna or planktonic communities (Chicharo et al., 2009b), as only the correlation with decreased abundance and composition of zooplankton can give us a clear image of their food resources.

The impacts of flow change are manifested across broad taxonomic groups including coastal and riverine plants, invertebrates and fish (Bunn *et al*., 2002). The changes in river inflow in our case lower water input in the coastal ecosystem can play a significant role on the reproduction of coastal species, limiting overall habitat availability (Bunn *et al*., 2002), higher temperatures can cause stratification, lower input of nutrients, higher retention time of organic matter, reduction in sediment input, longitudinal dispersal of migratory aquatic organisms (Bunn *et al*., 2002), declines in biodiversity and the alteration of natural food webs (Power *et al*. 1996) shifts in the water chemistry off coastal zones (Benstead *et al*., 1999), alterations in the distribution areas of zooplanktonic species (Kingsford *et al*., 1994; Chicharo *et al*., 2006a), invasions by alien species, effect on endemism (Bunn *et al*., 2002), changes in nutrient N:P:Si ratio can cause eutrophication by the toxic algae blooms as for instance dinoflagellates as it was discovered by (Rocha *et al*., 2002; reviewed by Chicharo *et al*., 2006b). The invasion and success of exotic and introduced species in rivers is facilitated by the alteration of flow regimes (Bunn et al., 2002). As a consequence of intense shipping and opening of new transport routes, brackish habitats have been increasingly effected by nonindigenous species (NIS) (Paavola et al. 2005). To what extent river flow modifications affect species diversity in the Guadiana Ecosystem has been previously evaluated by Muha et al. (2012). To what extent river flow contributes to the effectiveness of NIS as jellyfish species are remains unclarified.

The amount of precipitation rate influencing on the amount of river discharge is a consequence of Northern Atlantic Oscillation (NAO index) that has a significant impact on the precipitation in Southern Europe. A low-pressure system over Iceland and a permanent high-pressure system over the Azores control the direction and strength of westerly winds into Europe. If the index is low (NAO-), westerly's are suppressed and storms track southerly toward the Mediterranean Sea and increase the precipitation. When NAO is positive, there is less precipitation in Southern Europe. Since the NAO has the largest variability during the cold season, the loading pattern primarily captures characteristics of the cold season (NOAA, 2012). The correlation between NAO index and jellyfish abundance in Guadiana has been defined by Muha et al. (2012) though it would be interesting to know to what extent the precipitation rate influences on jellyfish dynamics on a wider scale.

Salinity gradient is a common feature of temperate estuaries having a pronounced spatial effect on the zooplankton composition and distribution (Azeiteiro et al., 1999). European brackish water seas (Baltic Sea, Black Sea and Sea of Azov, Caspian Sea) are subject to intense invasion of NIS (Paavola et al., 2005). In these seas, salinity is the most important range limiting factor and native species seem to reach a minimum species richness at intermediate salinities (Paavola et al., 2005). A critical physical barrier is absent and gives these species a clear advantage in surviving ballast water voyages and initial introduction into a brackish water area (Paavola et al., 2005) which seems to be the way of *B. virginica* introduction to Guadiana Estuary.

Salinity and temperature gradient changes in the estuarine zone are consequences of water discharge variability and are responsible for the movement of estuarine turbidity maximum (ETM) zone. The newly introduced jellyfish species have settled in brackish zone where there is highly productive ETM zone and it's theirs preferable habitat. In fact, in marine systems large aggregations of jellyfish are often found in areas of high turbidity and low light, where they have an advantage over visually feeding fishes (Eiane et al., 1999). A product of empty niches, suitable environmental conditions, and availability of proper vectors might be the most effective predictor for the invasibility of brackish water areas (Paavola et al., 2005). Lower densities of these species were noticed as well at lower or higher part of the estuary with different salinities ranging from 8- 28 PSU (Chicharo et al., 2009b) though in other research they have extended their presence from 3 to 35 PSU (Moore, 1987; Mills et al., 1995; Genzano et al., 2006). The brackish zone presents a focal area of presented model where predation impact by *B. virginica* is the most influential.

Blooms of jellyfish and ctenophores can attain enormous biomasses and cover extensive areas (Mills, 2001; Brodeur et al., 2002; Hay, 2006; Pitt et al., 2009). In many coastal and semi - enclosed areas (fjords, bays, and estuaries) gelatinous zooplankton are able to bloom and achieve enormous biomasses (tones per km 22) (Purcell, 2012, Brotz et al., 2012, Tinta et al., 2012). Jellyfish outbreaks can have many deleterious consequences, including losses in tourist revenue through beach closures and even the death of bathers (Purcel et al., 2007); power outages following the blockage of cooling intakes at coastal power plants (Purcel et al., 2007); blocking of alluvial sediment suction in diamond mining operations (Lynam et al., 2006); burst fishing nets and contaminated catches (Lynam et al., 2006); interference with acoustic fish assessments (Brierley et al., 2001); killing of farmed fish (Mills et al., 2001); reduction in commercial fish abundance through competition and predation (Lynam et al., 2006); and as probable intermediate vectors of various fish parasites (Hay et al., 2006, Richardson et al., 2009). Several studies had linked variations in jellyfish abundance with climate, particularly temperature and salinity (Purcell, 2005, 2007) however the processes at play can differ by region (Primo, 2012). Jellyfish have a major impact (large footprint) on lower trophic levels but translate relatively little production to higher levels in the food web (small reach) compared to forage fishes (Brodeur et al., 2007). Variety of *B. virginica* densities in the Guadiana Estuary can cause different responses to the well- established food web. Question remains what are the potential densities of the jellyfish that can cause deterioration or degradation of well- established food web in this estuarine area.

B. virginica feed primarily on pelagic invertebrates, although benthic/ epibenthic prey and larval fishes were also found in the gut contents in a research done by (Wintzer et al., 2013). Wintzer et al. (2013) has defined *B. virginica* as being a non- selective zooplankton predator. Stating that they are pelagic feeders, consuming both invertebrates and fish larvae. Copepod nauplii were by far most numerous prey in the guts, followed by cyclopoid copepods and mysids where all other prey items constituted less than 1% of the abundance in research done by Wintzer et al., (2013). Percent occurrence calculations for each item further support non-selective zooplankton feeding, with each prey item, except fish larvae, found in at least 50% of the sampling periods (Wintzer et al., 2013). Otherwise the analysis of the gut contents of this alien medusa by Mills et al. (1995) indicated that they feed nearly exclusively on small planktonic crustaceans and no fish larvae or eggs were seen in any of the stomachs. Wintzer et al. (2013) could not find a correlation between prey number and bell diameter because of the wide variety of prey types, including both larger (*i.e.* fish larvae, mysids) and smaller (*i.e.* nauplii) items. With the help of detailed sampling data available at the time of *B. virginica* presence there is a potential to build up a food- web model based on their predation success and prey availability.

Jellyfish biomass may decompose within the water column or on the benthos, depending on sinking rates and the depth of the water column as well as environmental conditions (Lebrato et al., 2011a, Tinta et al., 2012). Due to their high POC/PON and protein content, nutrient recycling after decomposition of these blooms cause large accumulations of inorganic nutrients to be released into the environment (Tinta et al., 2012), which can especially at stable no flux conditions further on cause eutrophication. The gelatinous biomass C/N is relatively low owing to a high nitrogen and low carbon content in the majority of the groups (C/N almost 20% lower than in other zooplankton groups, and overall it is between 10 and 20% lower than for phytoplankton and phytodetritus/ marine snow/ faecal pellets) (Lebrato et al., 2011a).

Recognition and knowledge on what to expect in the future is on a high priority list nowadays. Defining possible scenarios with a help of models is crucial for the further management conclusions. Jellyfish species have not been previously used in a food-web model of Guadiana Estuary. What are the potential scenarios remains to be clarified. This study focuses on the impact of a newly introduced species of jellyfish *B.virginica* on the well- established food- web using modeling approach. The significance of the present study is correlated to a very well documented and researched history of Guadiana before the disturbance of jellyfish and as well a continuous research of the jellyfish presence. Extential sampling data from year 1997 up to 2012 was conducted in Guadiana Estuary which data will be used through the process of statistical analysis for the model functioning. The abiotic conditions can significantly influence their dispersion which is evaluated through field sampling, statistical analysis and conclusively in a model. Our hypothesis is that climate-induced changes in ocean, biotic and abiotic conditions can cause variations in the amount of production that flows through the jellyfish population in the Guadiana Estuary. As *B. virginica* is newly introduced into the system we can study a potential reproductive and overall invasion success from its roots with the implementation of ‘If case situations- sensitivity analysis’ scenarios to better understand or avoid a collapse of an existing food web. Through the model we will try to evaluate to what extent do jellyfish, namely *B. virginica* affect the survival and growth of zooplankton, ichthyofauna such as sardines and anchovies, and indirectly on phytoplankton. We will define the amount of detritus produced by *B. virginica* under different scenarios in a model and individual detritus contribution of all individual groups of organisms. In the model we will evaluate how do fluctuations of organisms' biomass change over the extended variety of nutrient concentration and which species or group of marine organism becomes predominant under certain conditions. Using a theoretical top-down and bottom-up model, we will examine variability in the transfer of energy presented as biomass (mgC m-3) through alternate planktivore (jellyfish) pathways and use this to project possible changes in the food web within the estuary and coastal zone. With the use of bottom-up model we examine potential scenarios of varying energy flow through the jellyfish component and as well the influence of river flow dynamic on the entire food web. Well documented food web structures and alternate scenario strategies are being compared in the model. The mitigation measure is taken under consideration used through different water releases from the dam in order to measure the effects of such flow regulation to the downstream communities.

Methodology

Study area

The Guadiana Estuary constitutes the southern border between Portugal and Spain and its river basin is the fourth largest in the Iberian Peninsula, approximately 67 500 km2. The estuary is approximately 70 km long, encompassing a total area of 22 km2 and averaging 6.5 m in depth. It is a mesotidal estuary, with tidal amplitudes ranging from 1.3 to 3.5 m. The estuary is partially stratified when the average river flow (approx. 150 m3 s-1) and tidal prism (approx. 3×107 m3) occur (Morais et al., 2009). The climate of the area is classified as semi-arid Mediterranean with the driest months in July and August when the river flow is the lowest. It is marked by the severe draughts and heavy floods. Climate variability imposes a similar trend to river flow; thus, the average river inflows are as follows: dry years, 8–63 m3 s-1; average years, 170–190 m3 s-1; humid years, 412–463 m3 s-1 (Bettencourt et al., 2003, Morais et al., 2009). Historical data of the freshwater flow measured at the hydrometric station of Pulo do Lobo (37°48´N, 7°38´W), located a few kilometers above the last point of tidal influence (Mértola) and from the most upper sampling station (Alcotium), refers values ranging between 6.07 m3 s-1 and 2491.70 m3 s-1. Mean river flow varies considerably depending on the season and on the year (Ferreira *et al*., 2005). Strong interannual variation was also registered, being the average flow of the wettest year 436.4 m3 s-1 (in 1963/64), and 7.99 m3 s-1 in 1980/81 - the driest year recorded (Chicharo et al., 2009a). With the construction of the Alqueva Dam within this river basin in February 2002, which is one of the largest in Europe, those pulse events are smoothed (Machado et al., 2007).

Guadiana Estuary is divided into three sub-areas: upper with stations Alcotium and Gueirros do Rio; middle with sampling at Almada de Ouro and Foz de Odeleite; and lower estuary where samples were taken at Esteiro Carrasqueira, Barra, River Plume (Pluma) and Praia de St. Antonio station. This classification is commonly used to subdivide estuaries (Olausson et al., 1980, Chicharo et al., 2001a). Alcotium is considered as the uppermost station, situated in front of Alcotium (Portugal) at 38 km from the river mouth. The upper area is characterized by the freshwater dominance flow with salinity close to zero, where middle area is the salinity mixing zone (0.5- 25) and the lower part is characterized by the seawater intrusion dominance where salinity is above 25 (Chicharo et al., 2006a). The estuarine turbidity maximum zone before the dam filling was found between Foz de Odeleite and Almada de Ouro moving upstream to Guerrios do Rio after the closure. Presence of *B. virginica* normally takes place in brackish zone where ETM zone is present which is characterized by mixed salinity.

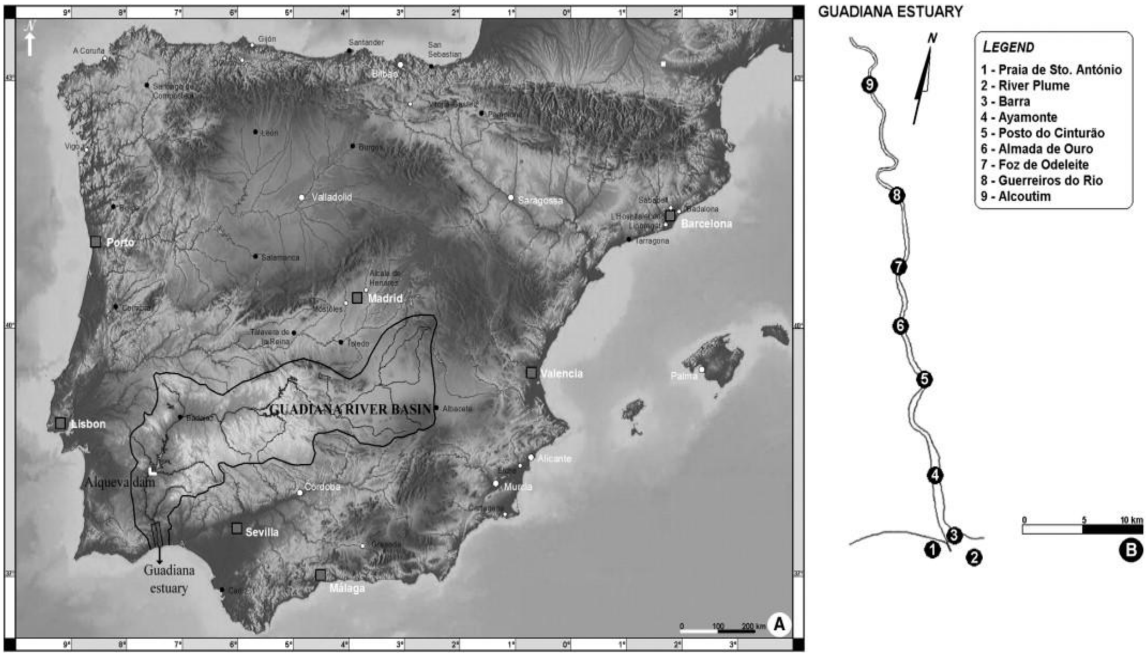

Figure 2- Guadiana river and estuary on the border between Spain and Portugal including sampling points (Morais et al., 2009).

Model run

The work was based on a theoretical non-dimensional model where we have evaluated biomass variations of each state variable under different scenarios (Figure 3). Presented possible scenarios are important factor for future management options. We can modify each individual state variable and relevant force in the model to see what could happen in certain case where models may combine several forces in continuous space and time. This gives as wider range and freedom compared to statistical models where only certain situation gives us a very narrow image of what is actually going on in the environment. Related literature to jellyfish presence and its impact on the environment is scarce and very much limited to statistics. Our trophic network model gives us new opportunity to evaluate the impact of jellyfish or other non-native species in hosting ecosystems which could guide decision makers towards mitigation or adaptation measures to limit the negative impact of these alien species.

We have developed a seasonal food-web model based on the annual occurrence of jellyfish *B. virginica*, which is from beginning of June to the end of August. We have used 6 functional groups of marine organisms gathered into state variables in the model. Groups of phytoplankton, zooplankton, ichthyoplankton (fish eggs and fish larvae separated), *B. virginica*, juvenile European anchovy (*Engraulis encrasicolus*) and their biomass, distribution, and diet were parameterized from survey data. In a model the energy flow of all state variables presented as biomass is simulated, where the competition between fish larvae and juvenile anchovy with *B.virginica* for the zooplankton is present as the only direct competitive process in a model. The interrelations between state variables are presented in the conceptual diagram (Fig. 3). We have gathered information based on surveys done from year 1997 until 2011 to evaluate abiotic parameters and simulate them in the model before the Alqueva dam in 2002. Occurrence of *B. virginica* was detected from year 2002-2011. Abiotic parameters were consistently measured for chlorophyll a concentration, densities of all state variables (ind. m-3), Secchi disk, dissolved oxygen, temperature, salinity, water discharge (m3 s-1) (annual monthly & summer gathered), organic mater, solid SSC (mg L-1) (total solid material- Seston) and NAO index. Central to our method is the representation of mass-balance trophic flows between functional groups for basic parameterization as it was previously done in other models (i.e. ‘Ecopath models’). These interactions are run in the model as part of time series dynamic where different abiotic parameters and its values are being part of limitations. We have incorporated the light intensity as a forcing affecting phytoplankton growth and bottom-up control of the food web. Second bottom-up abiotic forcing is water discharge (m3 s-1) influencing on the amount of nutrients and total solid material in the estuary. The water discharge was a consequence of different precipitation rate which were a reflection of NAO index. The use of NAO index was indirect where only the consequence of an increased or decreased amount of average annual and summer water discharge has been used as a forcing in the model. It thus not directly reflects the value of an index but only the pattern related to water discharge. This water discharge influences the amount of nutrients instantly. As for the fact that jellyfish contribute for large accumulations of inorganic nutrients we have incorporated detritus production into the food-web where the contribution of each individual state variable can be assessed.

For our theoretical network model we have worked on a predator- prey relation expressed with the Michaelis-Menten exponential (type II) response. One of the most popular mathematical model describing a predator-prey interaction is the following well-known Lotka-Volterra type predator-prey model with Michaelis-Menten (or Holling type II) functional response (Freedman, 1980, May, 1974):

$$\frac{d(x)}{dt} = ax(1 - x/K) - cxy/(m + x) \qquad eq.1$$

$$\frac{d(y)}{dt} = y\left(f\frac{x}{m+x} - d\right) \qquad eq.1$$

given that $x(0) > 0$ *and* $y(0) > 0$
where *x and y* stand for prey and predator density, respectively.
a,K, c,m,f,d are positive constants that stand for prey intrinsic growth rate, carrying capacity, capturing rate, half saturation constant, maximal predator growth rate, predator death rate, respectively (Hsu et al., 2001).

This functional response is the intake or release rate of a predator as a function of food density. It is associated with the numerical response which is the reproduction rate of a consumer as a function of food density. Three types of Holling's cycles are I, II, and III, where we focused on the second one, present a functional response which is characterized by a decelerating intake rate, which follows from the assumption that the consumer is limited by its capacity to process food (Holling, 1959). The losses of state variables’s biomass were mortality, respiration and excretion. Migration pattern was not included in the model for juvenile anchovy which needs for further discussion and development in future works. The energy flow within individual trophic groups follows a preposition:

Biomass (of state variables) = assimilation (or growth rate) - respiration - excretion - predation (mortality rate by predation) – mortality (non- predatory mortality rate);

where excretion, respiration and mortality are not uniquely used for all state variables.

Because jellies have higher water content than other groups (Shenker, 1985, Ruzicka et al., 2012), we transferred all weights into carbon content to avoid overestimation of jellyfish biomass. For all the groups in a model the densities and concentrations were converted into the same units of milligrams of carbon per cubic meter (mgC m-3), except nitrogen as major part of nutrients in (µmol m-3). It is conventional to report biomass of jellyfish as dry or elemental (e.g., C or N) mass, yet most models are constructed using wet weight (i.e., tonnes km-2) (Pauly et al., 2009). Often the units reported were wet or dry weight or number of individuals per unit volume along where the conversions were necessary. For other correlation factors the units were modified into same form, rate (per day). We used species or taxa-specific conversions to carbon weight and other conversions from variety of measures of ash free dry weight, dry or wet weight, jellyfish bell diameter or jellyfish length, growth rates, growth efficiencies, respiration rate, sloppy feeding, POC/ DOC excretion rates, assimilation efficiency, ingestion rates, half-saturation constants for predator- prey relationship, predation rate, clearance and exudation rates. Preference was given to equations and measures from studies taken in the vicinity of the studies ecosystem (e.g. Ria Formosa coastal lagoon in Portugal) or similar environment and global zone. Physiological rate parameters, growth efficiency and others were obtained from other ecosystem models, literature of compared measures or calculated from local and other relevant data. All the variables, coefficients and equations are found in tables 1, 2 and 3. Biomass values provided in table 1 are initial the lowest values of each state variable that was recorded in the same time of *B. virginica* presence that might be modified through different runs. These values might be modified later on through different runs and where the increase is stated separately at each run.

Conversions of individual parameter used in the model are found in annex I. In table 1 there are initial values of each state variables biomass. These values have been measured in the Guadiana and the lowest biomass presence in summer time was used for the initial biomass value in the model. Initial values of all state variables have been previously correlated to presence of *B. virginica.* Sampling data of state variables at the time when jellyfish was absent was not used, except in the model run when we have tested water discharge values and nutrient concentration in pre- dam situation. In table 3 there are all relevant differential equations each of them used in the model with 900 calculation loops through simulated 90 days.

Prey consumption rates by jellyfish can be estimated directly from gut contents (Purcell, 2003, Pauly et al., 2009), which in case of *B.virginica* was measured by Mills et al. (1995) and Wintzer (2013). Estimates of population production by jellyfish are rare and usually limited to rapid individual growth periods during the early phase of a cohort (Van der Veer et al., 1985, Olesen et al., 1994, Pauly et al., 2009). The diet of *B. virginica* was predisposed on the average feeding pattern by two studies (Wintzer et al., 2013, Mills et al., 1995) as measured predation rate and food type preferences. The diet breadth was broader by (Wintzer et al., 2013) than that found by Mills et al. (1995), in which 29 medusae from the Napa River fed exclusively on copepods, copepod nauplii, and barnacle nauplii. Samples by Mills et al. (1995) were collected on a single day late in the bloom season, which may explain the discrepancy. An average predation rate of both reviewed journals was used as an average prey type for further on calculation of prey biomass.

In order to calibrate our model statistical analysis were done using SPSS programme. Graphical representation of *B. virginica* density (ind. m-3) compared with abiotic components are discussed further on. Statistical analysis based on average abundance rate of *B. virginica* and zooplankton compared to abiotic conditions was done for an easier clarification and comparison with the results from the model. Statistical representations of results are an initial step towards the reliability of the model where both conditions are compared.

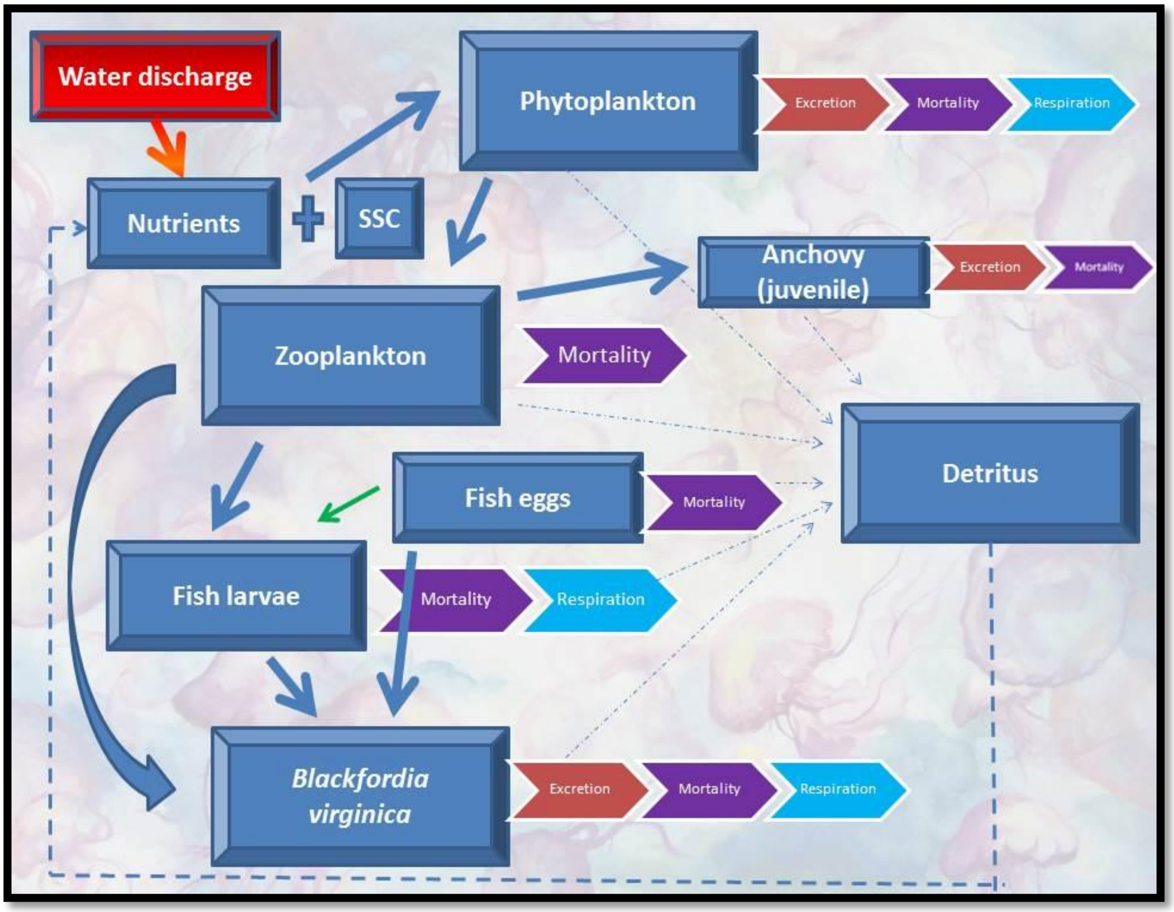

Figure 3- Conceptual diagram including all state variables used in the model, where narrow arrows represent predation, dotted arrows present dead organic material (detritus) contributing to detritus box.

Table 1- Variables, coefficients for the model of *Blackfordia virginica*

Coefficients	Definition	Units	Values (in.= initial)	References
Biotic, state variables				

BN	Initial concentration of nutrients (Nitrate)	µmol m-3	(from 0.0015 up to 0.6 tested in a model)	On site observations
satNP	Half-saturation constant* for phytoplankton with nitrate	µmol N_1	0.6	Chicharo et al., 2006a (Diatoms for nutrients)
SSC	Seston- organic material	mgC m-3	From 0.00002 up to 0.32	On site observations
kBN	Maximum uptake rate for diatoms	per day	0.8	Chicharo et al., 2006a
AssNP	Assimimation rate of nitrogen	per day	0.95	Calibration
BP	Initial biomass for phytoplankton	mgC m-3	1.34	On site observations
excp	Exudation constant for phytoplankton	per day	0.013	Nagata, 2000
RespP	Respiration constant for phytoplankton	per day	0.01	Kromkamp et al., 1995
kp1	Growth rate of phytoplankton	per day	0.9	Paerl et al., 2006
PredPZ	Grazing pressure	per day	0.29	Scavia et al.,

				1976
morp	Phytoplankton mortality not due to predation	per day	0.03	Scavia et al., 1976
satPZ	Half-saturation constant* for zooplankton in phytoplankton	mgC m-3	0.85	Jorgensen,1976
BZ	Initial biomass for zooplankton	mgC m-3	0.56	On site observations
MorZ	Mortality rate	per day	0.005	Chen et al., 1975
AssPZ	Assimilation rate of phytoplankton by zoo (at 20ºC)	per day	0.75	Di Torro et al., 1971
PredZI	Predation rate by ichthyoplankton	per day	0.074	Scavia, 1980
PredZB	Predation rate by *B. virginica*	per day	0.281	Wintzer 2013, Mills et al., 1995, modified
satZI	Half-saturation constant	mgC m-3	0.0062	Fortier et al., 1996
satZB	Half-saturation constant	mgC m-3	0.18	Wintzer, 2013, modified
BI	Initial biomass for Fish larvae	mgC m-3	0.02	On site observations
AssZI	Assimilation	per day	0.55	Govoni, 1986

	efficiency of zooplankton			
MorI	Mortality rate (for sardine postlarvae)	per day	0.012	Lenarz, 1972
RespI	Respiration rate of fish larvae	per day	0.01	Kiorboe,1987
PredIB	Predation rate of *B. virginica*	per day	0.05	Wintzer, 2013
satIB	Half-saturation constant fish larvae for *B. virginica*	mgC m-3	120.28	Calibration
BB	Initial biomass for *B. virginica*	mgC m-3	0.003	On site observations
RespB	Respiration rate	per day	0.014	Ishii et al., 2006
ExcB	Excretion rate	per day	0.0023	Calibration
AssZB	Assimilation efficiency of zooplankton by *B. virginica* (for other hydrozoa)	per day	0.68	Pitt et al., 2009
MorB	Mortality rate of *B. virginica*	per day	0.019	Calibration
AssIB	Carbon Assimilation rate of fish larvae by *B. virginica*	per day	0.81	Pitt et al., 2009
Beggs	Fish eggs	mgC m-3	0.02	On site

	biomass			observations
keggs	Growth rate of fish eggs	per day	0.08	Kneib, 1993
Meggs	Mortality rate fish eggs	per day	0.007	Kneib, 1993
BBG	Hatching rate success to fish larvae	per day	0.025	On site observations
satBeggsBB	Half saturation concentration of fish eggs	mgC m-3	0.0005	Calibration
sateggs	Half-saturation constant	mgC m-3	1.35	Calibration
PredIEB	Predation rate of *B. virginica* on fish eggs	per day	0.1	Mills et al., 1995, modified
AssIEB	Assimilation efficiency of *B. virginica* for fish eggs	per day	0.905	Pitt et al., 2009
BJ	Initial biomass for *Engraulis encrasicolus*- juvenile anchovy	mgC m-3	0.002	On site observations
satZJ	Half-saturation rate for anchovy	mgC m-3	0.4	Monteiro, 2001
AssZJ	Assimilation efficiency of zooplankton by	per day	0.8	Monteiro, 2001

	juvenile anchovy			
PredZJ	Predation rate for juvenile anchovy	per day	0.25	Monteiro, 2001
ExcJ	Excretion rate for juvenile anchovy	per day	0.01	Monteiro, 2001
RespJ	Respiration rate for juvenile anchovy	per day	0.15	Oguz et al., 2008
MorJ	Mortality rate for juvenile anchovy	per day	0.02	Oguz et al., 2008

* Half-saturation constant for the ith predator, which is the prey density at which the functional response of the predator is half maximal.

Table 2- Variables, for abiotic coefficients for the model of *Blackfordia virginica*

Abiotic variables, coefficients				
IE	Light intensity-Mean sunlight hours per day in Algarve (Jun-August)=10 hours	Hour	10/ 14 sunlight/darkness	http://www.sagres.climatemps.com/
Q	Water discharge into the Estuary	m3 s-1	Variable	

Model run works through a repeatedly set of equations based in a loop system with repeated frequency of 900 times calculations (Table 3). Each set of equation from the initial nutrient equation to final detritus production is correlated within the whole system.

Correlations between the equations in the model are based on the conceptual diagram. Light limitation equation is based on the amount of light availability through day time sinusoidal change for the summer time in the Algarve. It is directly influencing phytoplankton growth. Nutrient concentration (nitrate) is represented correspondently to the amount of water discharge as part of the nutrient equation where initial concentration of nutrients (nitrate) (µmol m-3) is measured based on the average of summer monthly water discharge (m3 s-1) to corresponding concentration of nitrate (µmol m-3). Same evaluation is done for the seston which is representing the amount of solid organic material that enters the system. Detritus in the conceptual diagram represents the dead organisms, as well the equation for detritus is only the production of dead organic material and the final amount is not recycled within the food web. We did incorporate the previously averaged amount of seston (solid organic material) as part of the first nutrient/ water discharge equation. It is though a simplified version of the amount available per cubic meter. The simplification is done from a reason that unknown amount of detritus is transferred out of the estuarine ecosystem. All the correlations are represented in the Table 3. This equation is correlated to phytoplankton Michaelis- Menten equation and is forcing phytoplankton growth by nutrient availability. Set of equations is written by the coefficients represented in Table 1. The coefficients tend to be unmodified unless specifically stated at each initial model run. Model runs were based on variations of sensitivity tests. For each sensitivity test there were changes done at the bottom of the food web as different amount of nutrients available for phytoplankton. For some sensitivity tests there were different initial biomass of individual group used and nutrient amount was on its average after dam closure.

Table 3- Differential equations for the model

Limitations in a model, forces:
Light limitation:

$$\mathrm{lE(i)} = \sin(\mathrm{x(i)} \times 2 \times \mathrm{pi} - 2 \times \mathrm{pi} * 14/24) \qquad eq.2$$

kp=kp1*lE;   where light limitation equation is directly related to phytoplankton growth rate

Nutrient (nitrate) concentration values corresponding to the average summer water discharge:
<u>Before the dam:</u>
38 m3 s-1=0.06 µmol m-3
27 m3 s-1=0.025 µmol m-3
15 m3 s-1=0.009 µmol m-3

<u>After the dam:</u>
7.5 m3 s-1=0.004 µmol m-3
4.4 m3 s-1=0.007 µmol m-3
3.75 m3 s-1=0.001 µmol m-3
2.75 m3 s-1=0.0015 µmol m-3

Seston- suspended solid organic material: Average of SSC (mg m-3) corresponds to average summer monthly water discharge (m3 s-1).

<u>Before the dam:</u>
38 m3 s-1=0.032 mg m-3
27 m3 s-1=0.02 mg m-3
15 m3 s-1=0.0145 mg m-3

<u>After the dam:</u>
13 m3 s-1=0.000005 mg m-3

9 m3 s-1=0.000672 mg m-3
7.5 m3 s-1=0.000023 mg m-3
2.7 m3 s-1=0.000018 mg m-3

Michaelis-Menten type 2 response:

Nutrients:

$$DBN/\partial t = kBN \times \partial BN/\partial t\ - (kp \times \partial BN/\partial t \times \partial BP/\partial t\ /satNP + \partial BN/\partial t) + SSC$$

eq. 3

where $\partial BN/\partial t$ = nitrogen concentration variation through time series, *kp*= growth rate of phytoplankton based on light availability, $\partial BP/\partial t$= phytoplankton biomass variation through time series, *satNP*= half-saturation constant for the ith predator, which is the prey density at which the functional response of the predator is half maximal (for phytoplankton incorporation of nitrogen), *SSC*= Suspended solid organic material (mgC m-3). The rest of equations are calculated using same procedure, with different coefficients and their description written in table 1.

Phytoplankton:

$$\partial P/\partial t = (AssNP * kp * \partial BN/\partial t * \partial BP/\partial t\ /(satNP + \partial BN/\partial t)) - ((PredPZ * \partial BP/\partial t * \partial BZ/\partial t)/(satPZ + \partial BP/\partial t)) - (excp + RespP + morp) * \partial BP/\partial t$$

eq.4

Zooplankton:

$$\partial Z/\partial t = ((AssPZ * PredPZ * \partial BP/\partial t * \partial BZ/\partial t)/(satPZ + \partial BP/\partial t)) - ((PredZI * \partial BZ/\partial t * \partial BI/\partial t)/(satZI + \partial BZ/\partial t)) - ((PredZB * \partial BZ/\partial t * \partial BB/\partial t)/(satZB + \partial BZ/\partial t)) - ((PredZJ * \partial BZ/\partial t * \partial BJ/\partial t)/(satZJ + \partial BZ/\partial t)) - MorZ * \partial BZ/\partial t$$

eq. 5

Ichthyoplankton:

Fish larvae:

$$\partial I/\partial t = ((AssZI * PredZI * \partial BZ/\partial t * \partial BI/\partial t)/(satZI + \partial BZ/\partial t)) + (BBG * \partial BI/\partial t * \partial Beggs/\partial t/(satBeggsBB + \partial Beggs/\partial t)) - ((PredIB * \partial BI/\partial t * \partial BB/\partial t)/(satIB + \partial BI/\partial t)) - (RespI + MorI) * \partial BI/\partial t$$

eq.6

Fish eggs:

$$\partial IE/\partial t = keggs * \partial Beggs/\partial t - (BBG * \partial Beggs/\partial t * \partial BI/\partial t/(satBeggsBB + \partial Beggs/\partial t)) - ((PredIB * \partial Beggs/\partial t * \partial BB/\partial t)/(sateggs + \partial Beggs/\partial t)) - Meggs * \partial Beggs/\partial t$$

eq. 7

***Engraulis encrasicolus*- juvenile european anchovy:**

$$\partial AJ/\partial t = ((AssZJ * PredZJ * \partial BZ/\partial t * \partial BJ/\partial t)/(satZJ + \partial BZ/\partial t)) - (ExcJ + MorJ) * \partial BJ/\partial t;$$

eq. 8

***Blackforida virginica*:**

$$\partial B/\partial t = ((AssZB * PredZB * \partial BZ/\partial t * \partial BB/\partial t)/(satZB + \partial BZ/\partial t)) + ((AssIB * PredIB * \partial BI/\partial t * \partial BB\partial t)/(satIB + \partial BI/\partial t)) + ((AssIEB * PredIEB * \partial Beggs/\partial t * \partial BB\partial t)/(sateggs + \partial Beggs/\partial t)) - (RespB + ExcB + MorB) * \partial BB/\partial t$$

eq. 9

Detritus:

All state variables joint together:

$$\partial Det/\partial t = (excp + morp) * \partial BP/\partial t + MorZ * \partial BZ/\partial t + (MorI) * \partial BI/\partial t + (ExcB + MorB) * \partial BB/\partial t + Meggs * \partial Beggs/\partial t + (ExcJ + MorJ) * \partial BJ/\partial t$$

eq. 10

Each individual group:

$\partial DetBPt/\partial t = (excp + morp) * \partial BP/\partial t$; Detritus from Phytoplankton

$\partial DetBZ/\partial t = (MorZ * \partial BZ/\partial t$; Detritus from Zooplankton

$\partial DetBI/\partial t = (MorI) * \partial BI/\partial t + Meggs * \partial Beggs/\partial t$; Detritus from Ichthyoplankton

$\partial DetBB/\partial t = (ExcB + MorB) * \partial BB/\partial t$; Detritus from *B. virginica*

$\partial DetBJ/\partial t = (ExcJ + MorJ) * \partial BJ/\partial t$; Detritus from Juvenile anchovy

eq. 11

The average annual river water discharge after the Alqueva dam in years of *B. virginica* presence were 27.913 m3 s-1 (2002), 17.729 m3 s-1 (2008), 16.7 m3 s-1 (2009) and 191.235 m3 s-1 (2011). NAO index correspondingly to same years was 0.72 (2002), 2.1 (2008), -0.41 (2009) and -1.9 (2011). The average summer water discharge is significantly lower in years after the Alqueva dam, with the exception of year 2011 due to high winter precipitation rate. *B. virginica* was not present before the dam closure but after 2002 there is a gradual increase of its biomass over years (Fig. 4). In the final sampling year of 2011 the density was low (below 5 ind. m-3) and it was found only at the mouth of the estuary. There is a strong inverse correlation between the *B. virginica* density and annual water discharge (Fig. 5) and strong positive relation to the NAO index with the abundance of jellyfish (Fig. 6). There is a positive correlation between the low density of zooplankton and high density of *B. virginica* where all zooplanktonic species are joint together (Fig. 7). Looking through species compositions comparing each individual station between each other there seems to be a correlation between lower species richness and higher evenness of zooplankton at the stations where there was also presence of the most abundant adult cnidarians *B. virginica.* These results are not presented in statistical section but its percentages of species composition are used and recalculated in the calibration for the model. The strong correlation between water discharge, zooplankton and *B. virginica* density must not be overlooked where similarity of trends noticed between zooplankton density and water discharge are significant.

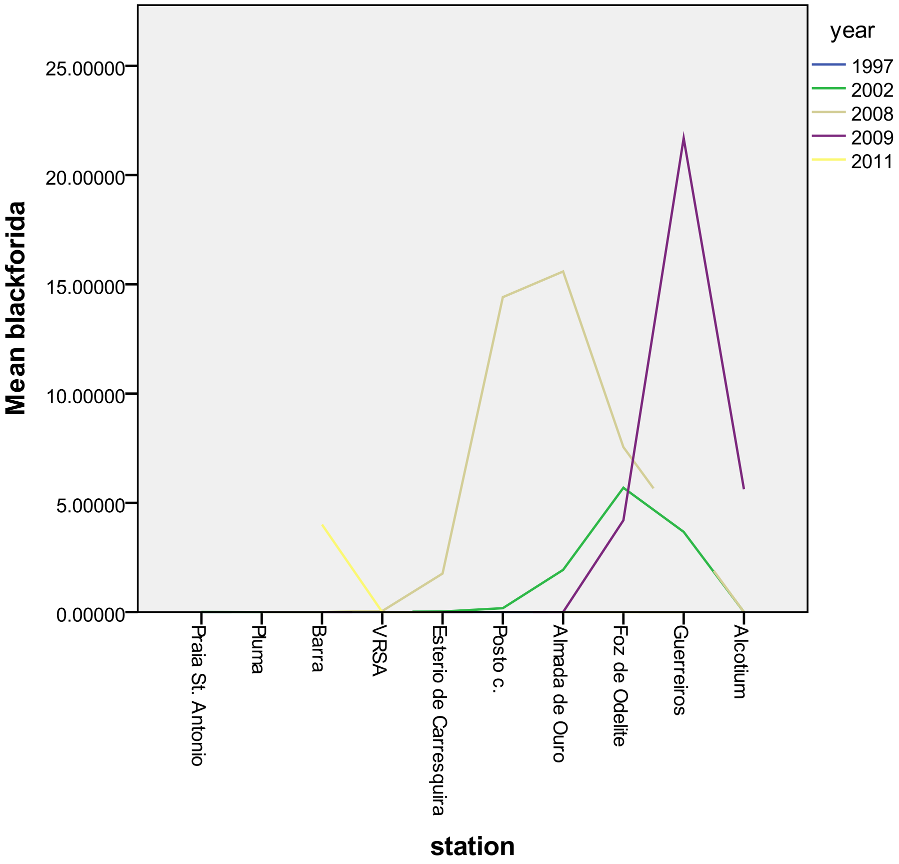

Figure 4- Average of *B. virginica* (ind. m-3) densities through presented years at each individual sampling station.

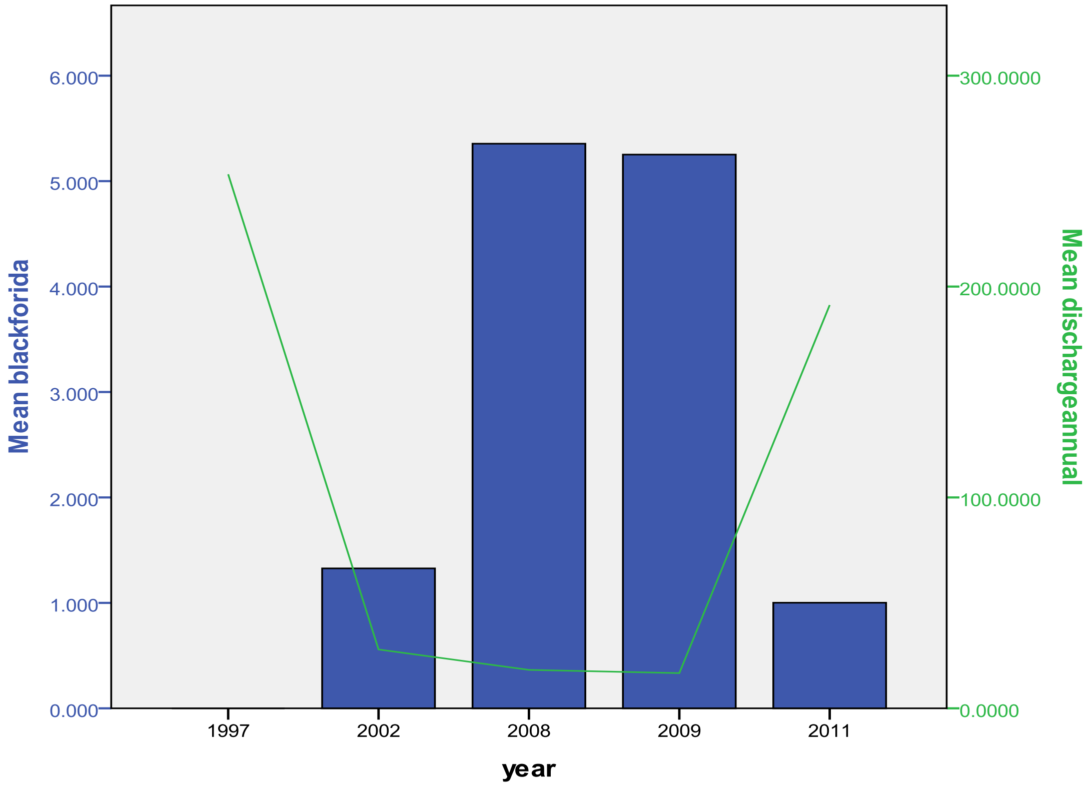

Figure 5- Mean abundance of *B. virginica* (individual's m-3) compared to mean annual water discharge in winter Q (m3 s-1) from year 1997 up to 2011.

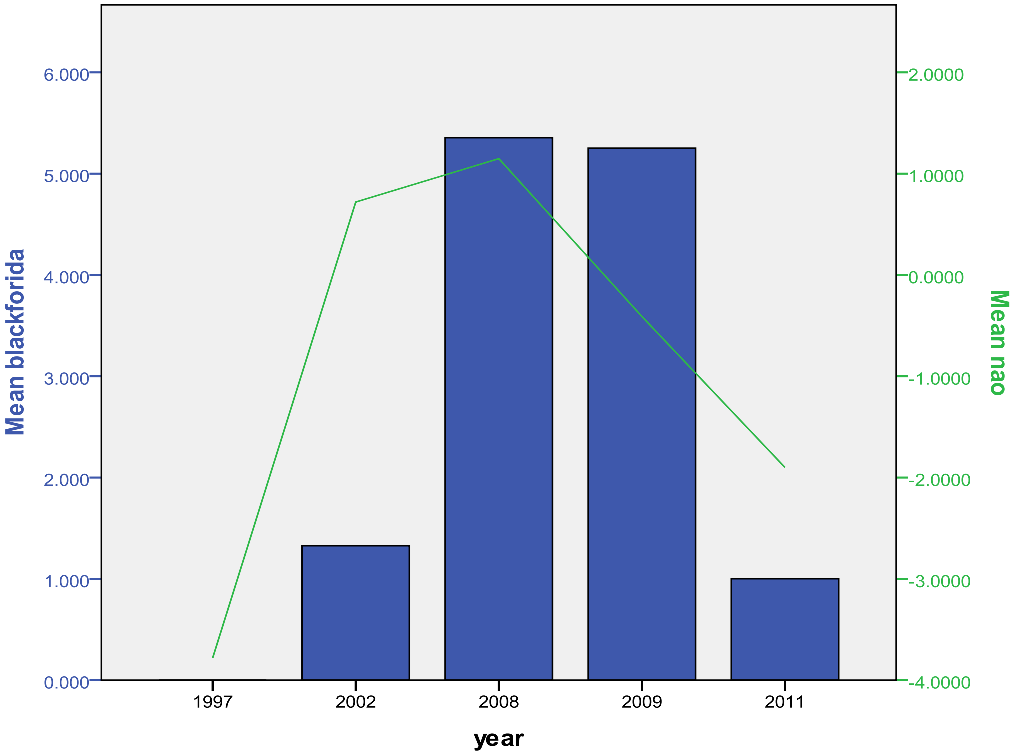

Figure 6- Mean abundance of *B. virginica* (individual's m-3) compared to mean NAO (North Atlantic Oscillation) index from year 1997 up to 2011.

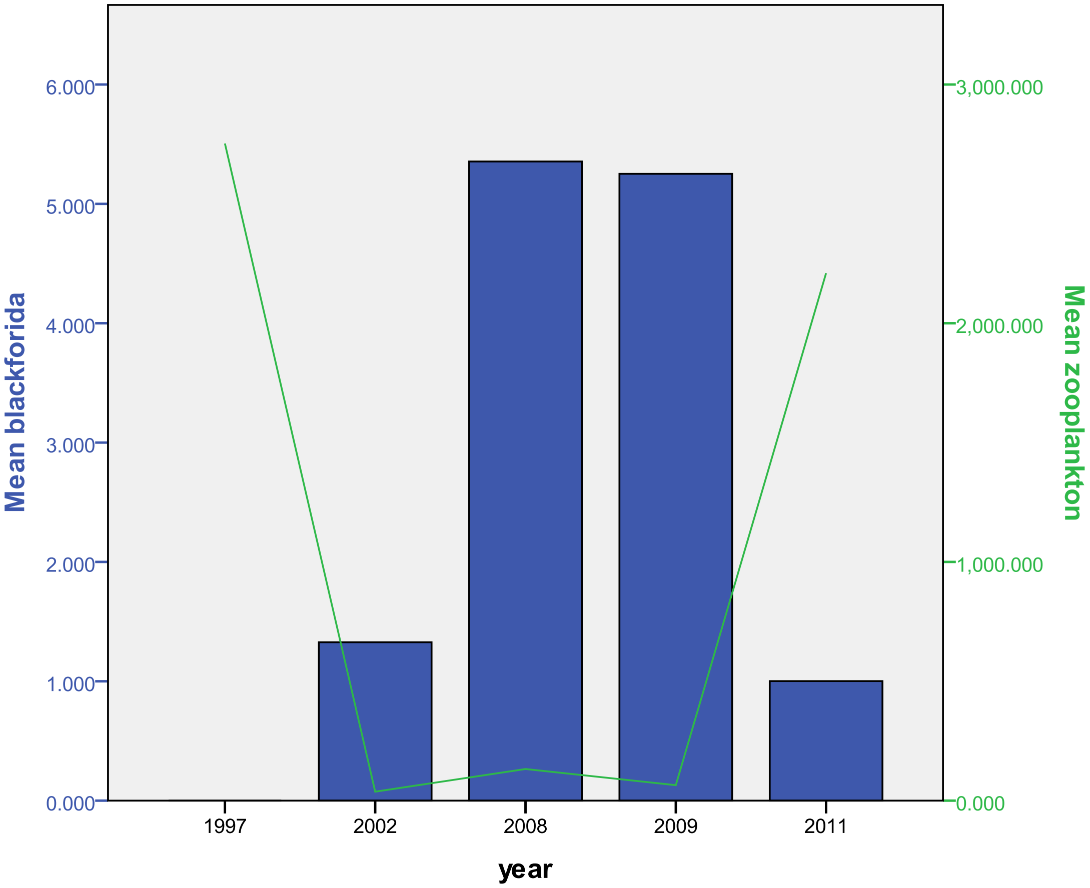

Figure 7- Mean abundance of *B. virginica* (individual's m-3) compared to mean zooplankton abundance (individuals m-3) between years 1997 up to 2011.

Variation of phytoplankton biomass highly reflects variation of light availability within day and night cycle. Light intensity through the day and night cycle gradually changes from 0 to 1 during the 90 summer days cycle with accuracy of 2.4 h modification (Fig. 8). The frequency of 2.4 hours stays the same for each individual state variable recalculated through sets of equations. This defines certain sensitivity for each individual daily cycle of provided results in the model.

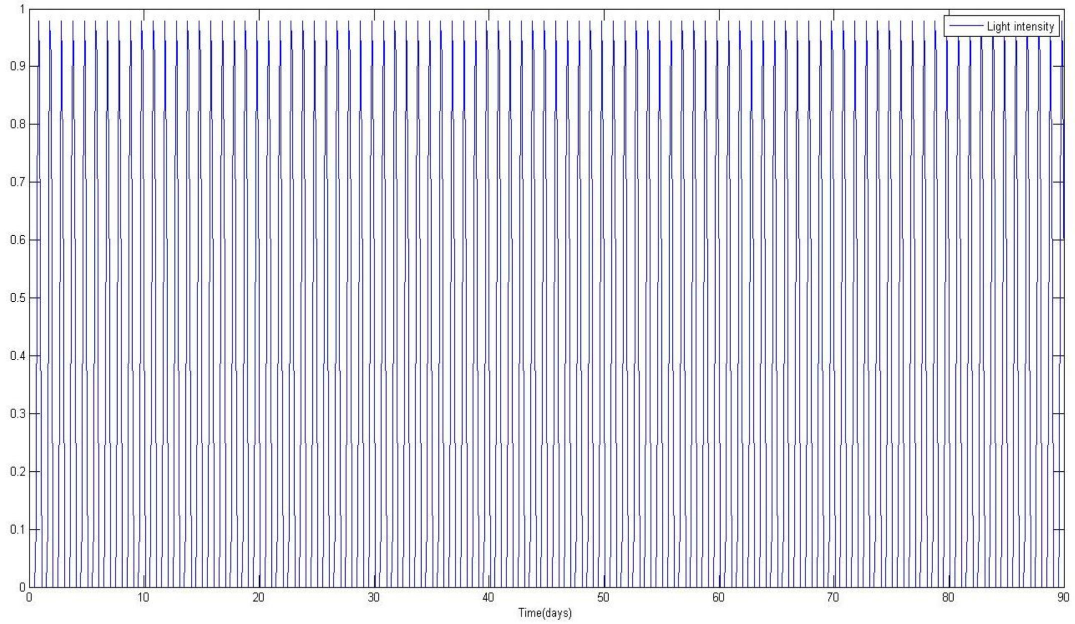

Figure 8- Light intensity variation through time series of 90 days.

1. Run 1, after dam, Q (summer discharge)=7.5 m3 s-1, BN =0.004 µmol m-3, SSC=0.00003 mg m-3

In this situation with low nutrient conditions the phytoplankton, fish eggs, fish larvae and *B. virginica* biomass increases through summer but zooplankton and juvenile anchovy biomass decreases (Fig. 9 and Fig. 10). Phytoplankton biomass stays low over the summer from 0.009 up to 0.9 mgC m-3 in first 70 days of model run which is related to efficient amount of predation pressure from zooplankton. After that the phytoplankton increases up to 250 mgC m-3. Zooplankton in the end of the summer time decreases after the initial rise up to 2 mgC m-3 to values of biomass that does not present significantly important contribution to the food web. The initial rise of zooplankton corresponds to the abundance of 4300 ind. m-3. This abundance corresponds to the measured densities in years with low water discharge especially the low biomass situation after first 30 days when the biomass is half of its maximum (Fig. 5 and Fig. 7). Biomass of fish eggs gradually increases up to 1 mgC m-3 (Fig. 11) where the constant contribution of fish eggs is included in the model through whole summer. Detritus contribution from all state variables stays low over the summer from 0.06- 0.7 mgC m-3 and increases in the end of the summer up to 9 mgC m-3 which is strongly related to increased phytoplankton biomass (Fig. 14). The average detritus production over summer still remains higher for 10 or 100 fold increase than measured in years of low nutrient contribution. The largest contribution of detritus comes from phytoplankton (Fig. 13). The other groups contribute similar amounts around 0.005 mgC m-3. *B. virginica* biomass increase is correlated to decrease of zooplankton in first half of the summer, after that the biomass of fish eggs and fish larvae represent their main food source as zooplankton becomes depleted (Fig. 15). The highest achieved biomass is 0.45 mgC m-3 which corresponds to 750 ind. m-3 not yet measured abundance in Guadiana where the highest values (31.1 ind. m-3) measured in low water discharge conditions were in 2008 (Fig. 4).

After the initial increase the biomass of jellyfish drops and stays on the some level between 0.3-0.18 mgC m-3 which does present 10 fold increase to the measured rates in the Guadiana with similar nutrient conditions. Comparing the predational success between fish larvae group and jellyfish (Fig. 15), jellyfish tend to be much more successful as they their initial biomass is lower than fish larva but their predational impact is higher as their major increase compared to fish larvae is for 0.35 mgC m-3 higher in the middle of the summer. Juvenile anchovy *Engraulis encrasiocolus* biomass starts to decrease in the middle of summer due to depleted prey, zooplankton biomass (Fig. 12). The highest achieved value of 1.45 mgC m-3 drops to similar measured values in Guadiana. There is no significant difference of its biomass through the summer. The migration of juvenile anchovy in the end of the summer out of the estuary is not included in the model. In that case the zooplankton biomass would be higher in the second half of the summer.

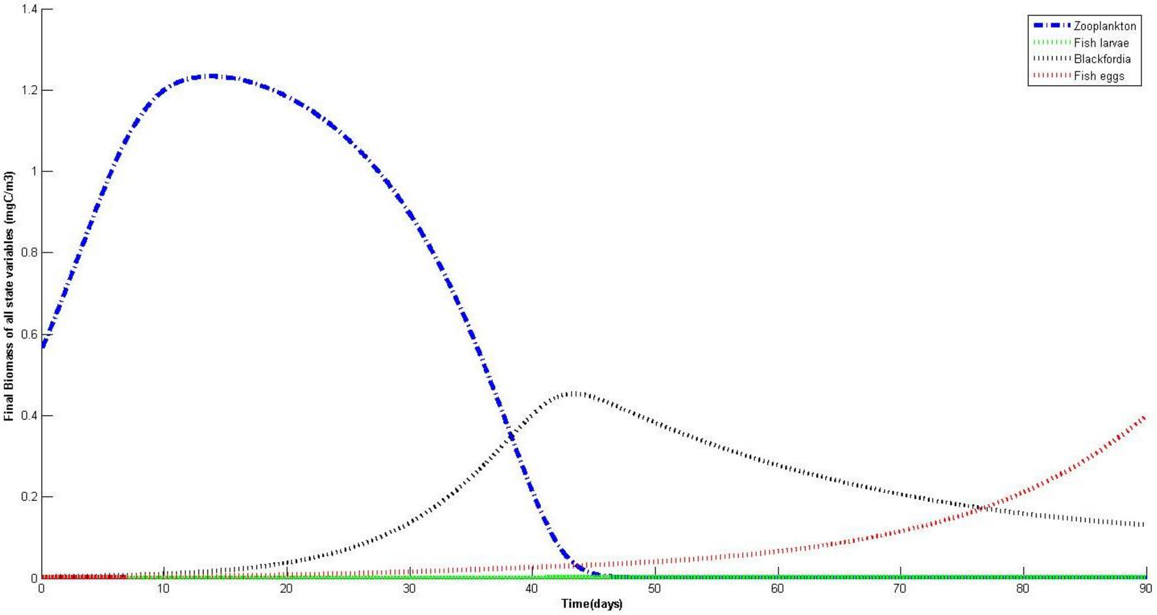

Figure 9- Biomass variation of organic carbon of each individual group (mgC m-3) in the Guadiana Estuary over period of 90 days under conditions of run 1.

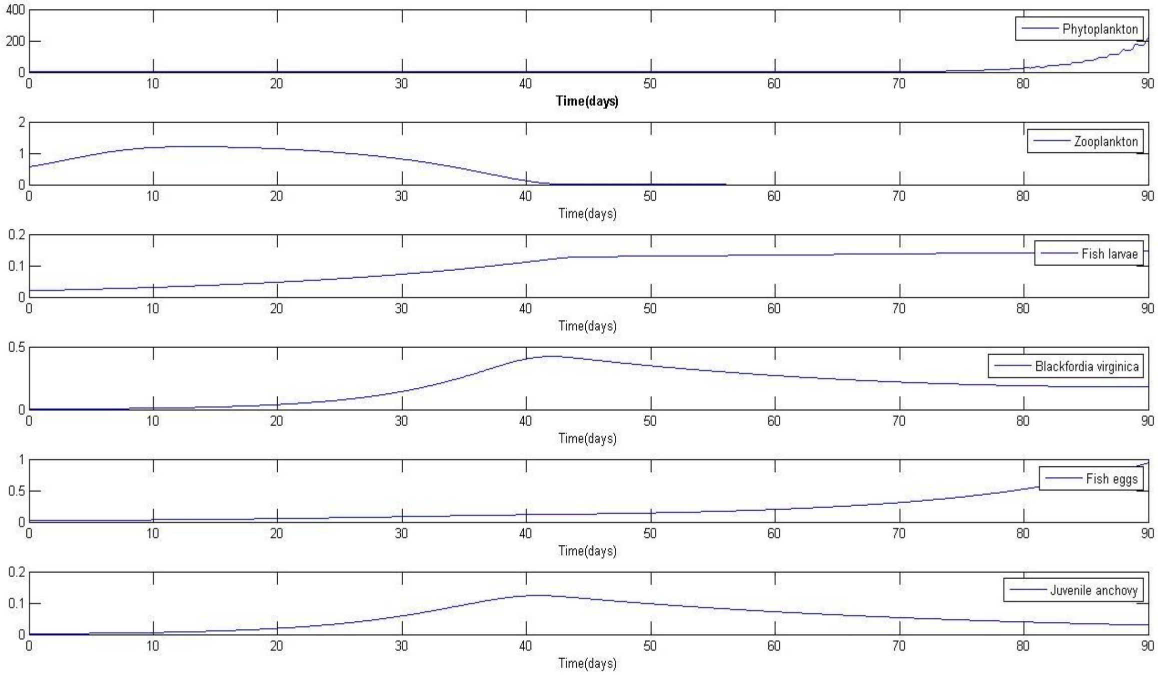

Figure 10- Biomass variation of phytoplankton (mgC m-3), zooplankton, fish larvae, *B. virginica*, fish eggs and juvenile anchovy (mgC m-3) through time series of 90 days in summer conditions and nutrients availability by run 1.

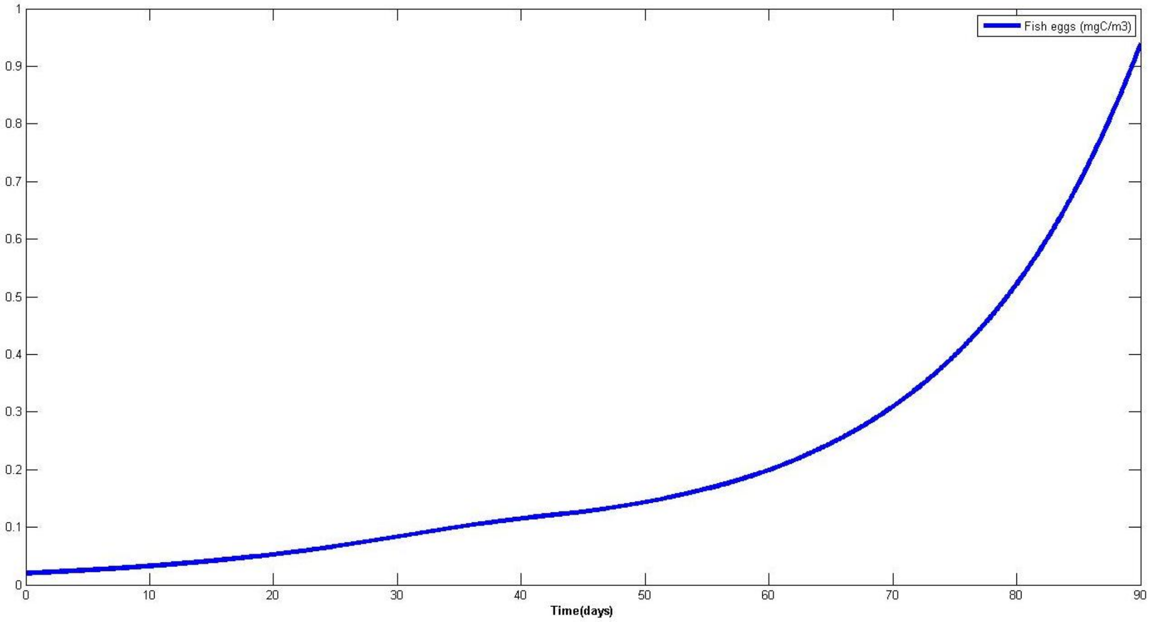

Figure 11- Biomass variation of fish eggs (mgC m-3) through time series of 90 days in summer conditions and nutrients availability by run 1.

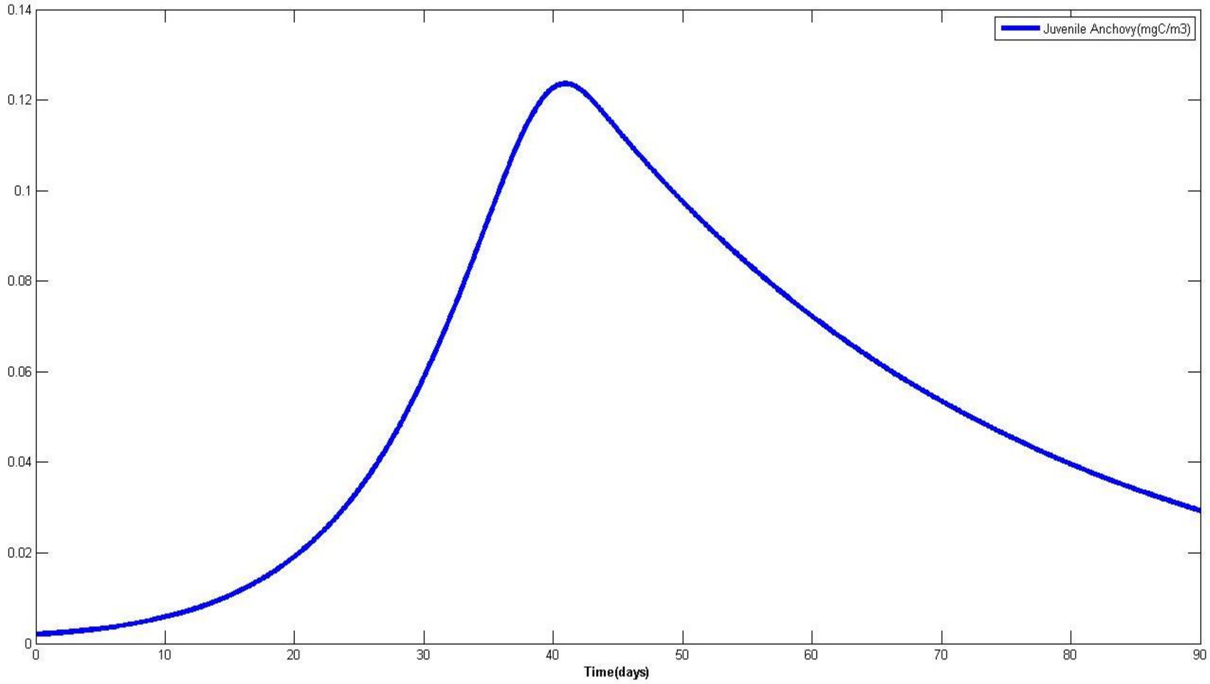

Figure 12- Biomass variation of juvenile anchovy *Engraulis encrasiocolus* (mgC m-3) through time series of 90 days in summer conditions and nutrients availability by run 1.

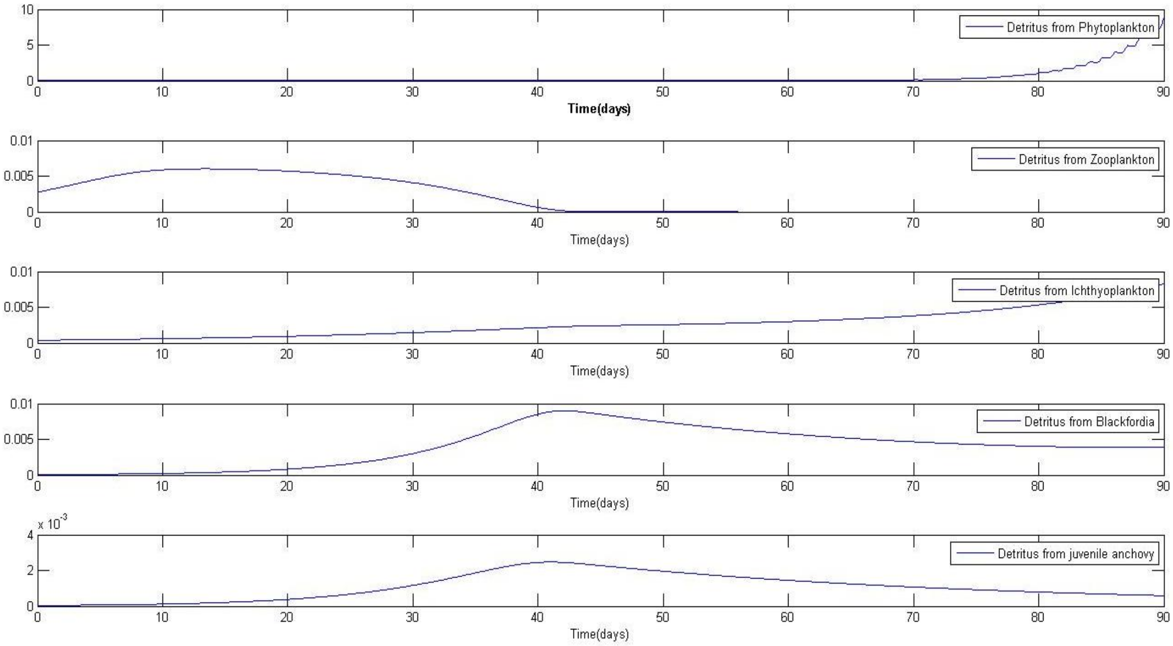

Figure 13- Detritus production as organic carbon content of phytoplankton (mgC m-3), zooplankton, ichthyoplankton (fish larvae and fish eggs), *B. virginica* and juvenile anchovy (mgC m-3) through time series of 90 days in summer conditions and nutrients availability by run 1.

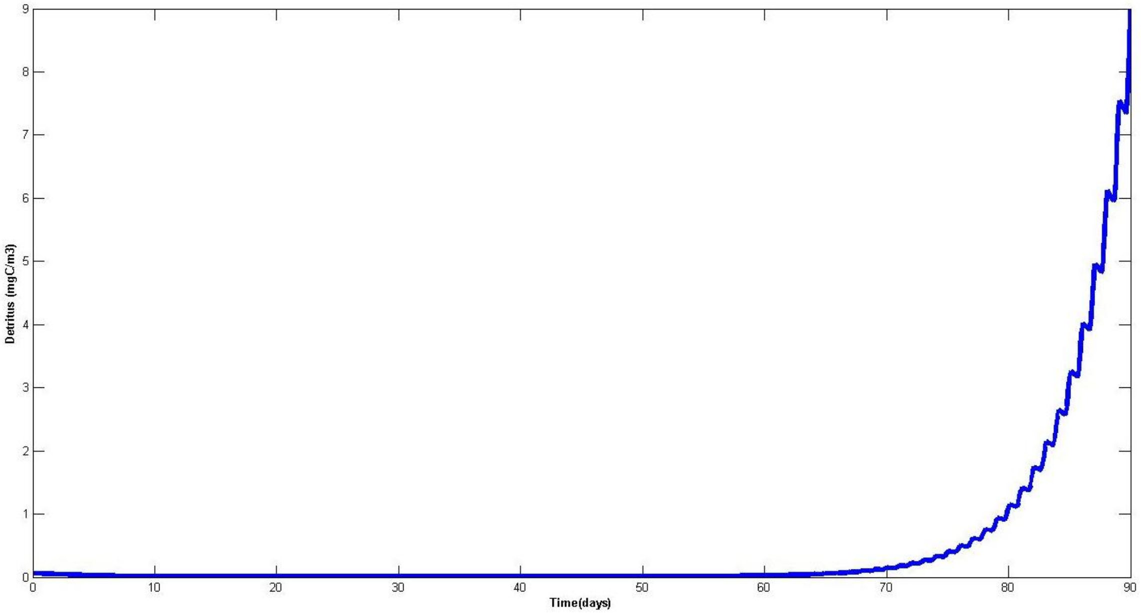

Figure 14- Total detritus production (mgC m-3) jointly together by all state variables in through summer time by nutrient availability in run 1.

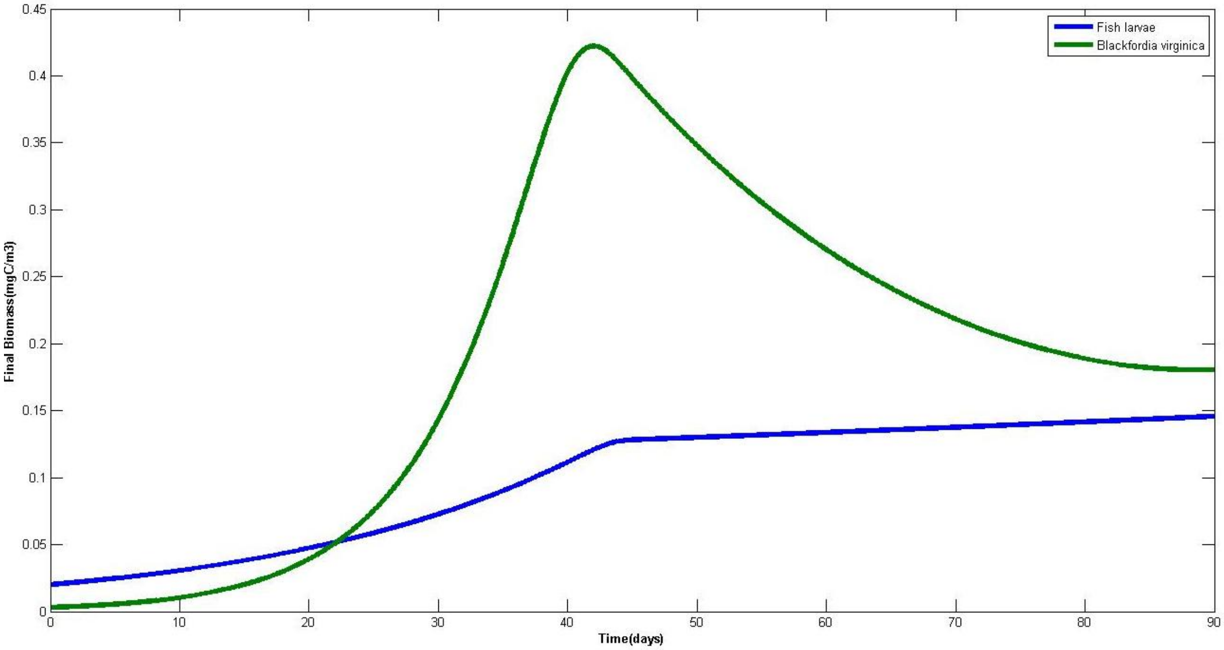

Figure 15- Biomass variation of fish larvae and *B. virginica* (mgC m-3) through time series of 90 days in summer conditions and nutrients availability by run 1.

2. Run 2, after dam, Q (summer discharge)= 2.75 m3 s-1, BN =0.0015 μmol m-3, SSC=0.00002 mg m-3

The nutrient amount did not differ greatly from the previous run 1. In run 1 there is higher phytoplankton biomass in the system compared to run 2 where the highest values in the end of the summer are 150 mgC m-3 (Fig. 17). Slight decrease in nutrient availability corresponds to slight decrease of phytoplankton and zooplankton biomass but does not differ greatly on other state variables as for instance fish larvae and *B. virginica* (Fig. 18). This situation corresponds to similar condition with very low nutrient amount in year 2009 when the highest biomass of jellyfish was present at the upper part of the estuary Gueirros do Rio (Fig. 4). Trails of varieties of low water discharges (below 12 m3 s-1) without additional nutrient loading from anthropogenic activities results in some pattern dynamics of all state variables similar to presented run 1 and 2 (Fig 9 and Fig. 16). Juvenile anchovy have the lowest biomass by the end of the summer in the estuary 0.01-0.03 mgC m-3 (Fig. 17). As previously stated the migration of juvenile out of the estuary in the end of the year is not included in the model thus imposes an error. In this case juvenile anchovy biomass is lost of the system as well by the end. In case of increasing predation pressure of *B. virginica* over zooplankton the model appears highly sensitive and this predation effect has an impact over the wide range of all state variables with higher decrease of other predatory groups over zooplankton. Patterns of all state variables as well as their detritus production stay the same in run 2 as presented in run 1.

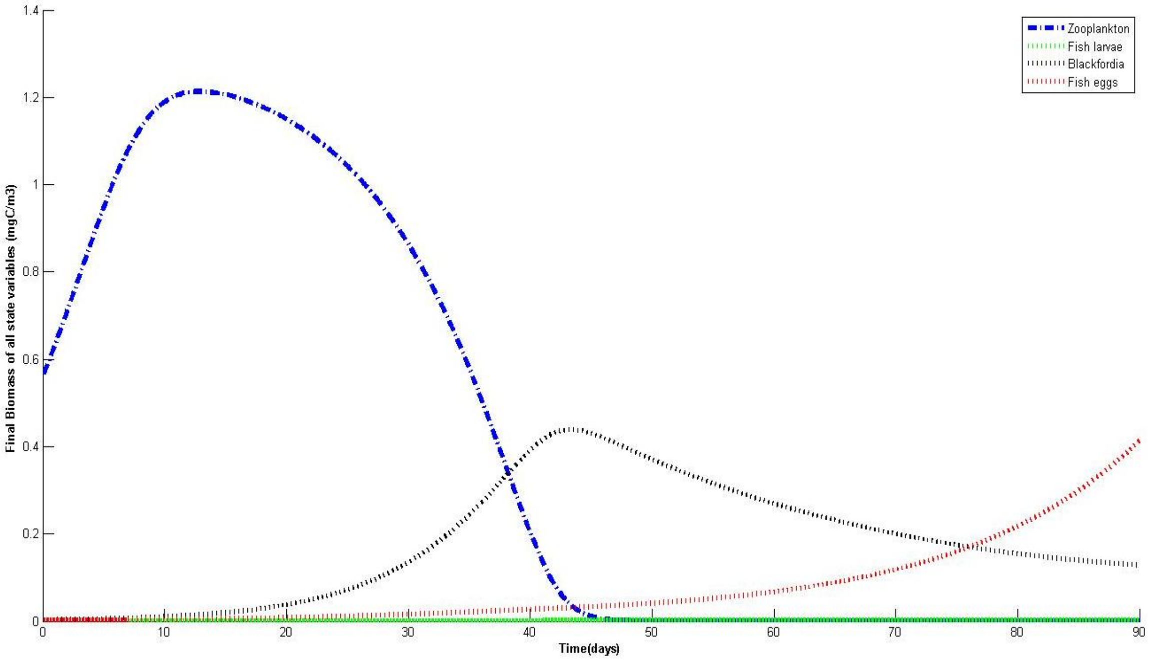

Figure 16- Biomass variation of organic carbon of each individual group in the model over period of 90 days under conditions of 2 run.

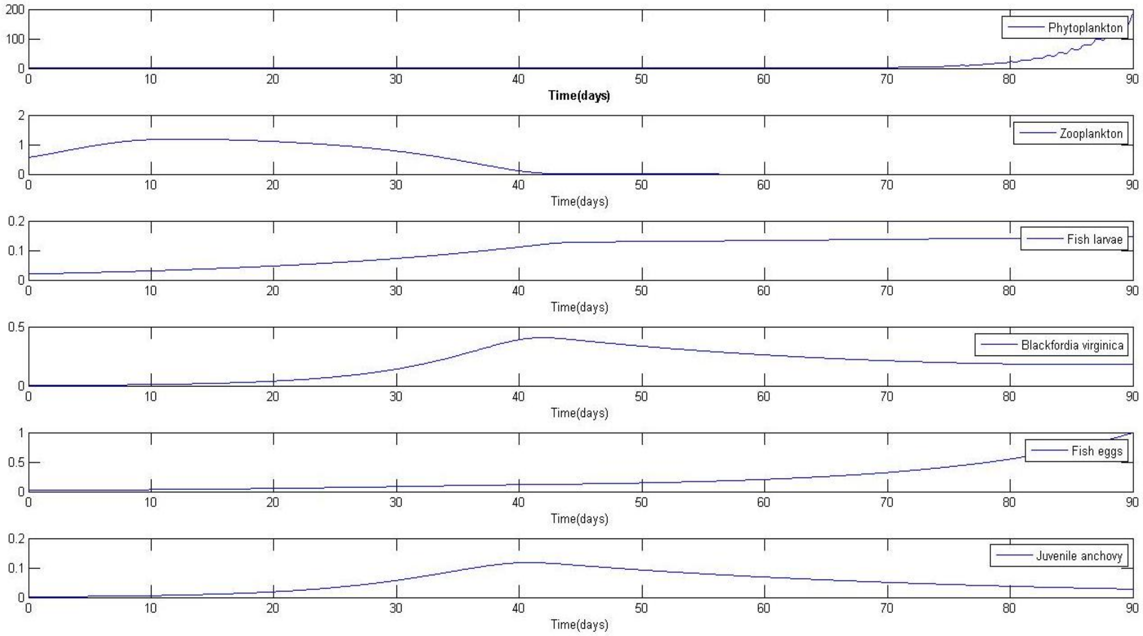

Figure 17- Biomass variation of phytoplankton (mgC m-3), zooplankton, fish larvae, *B. virginica*, fish eggs and juvenile anchovy (mgC m-3) through time series of 90 days in summer conditions and nutrients availability by run 2.

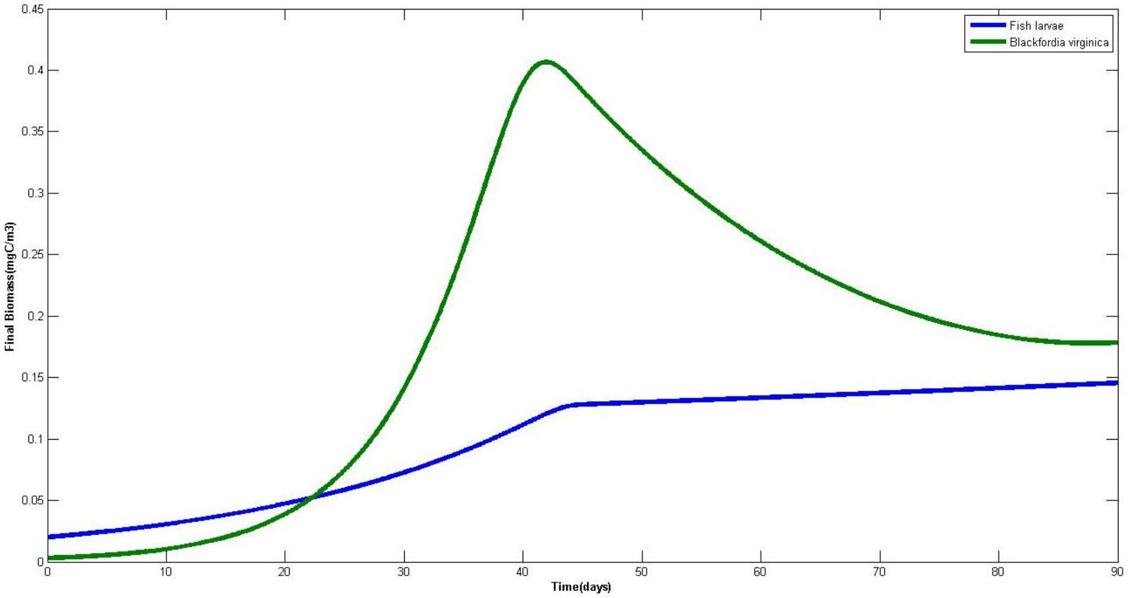

Figure 18- Biomass variation of fish larvae and *B. virginica* (mgC m-3) through time series of 90 days in summer conditions and nutrients availability by run 2.

3. Run 3 has some conditions as run 2 (BN =0.0015 µmol m-3, SSC=0.00002 mg m-3- low nutrient conditions) but there is an increase in initial levels of *B. virginica* from 0.003 to 0.03 mgC m-3.

In case of higher initial values of jellyfish the phytoplankton increases up to 4.5* 10^4 mgC m-3 (Fig. 19) which correspond in the predominance of the phytoplankton group by the end of the summer. The situation appears similar to the situation with increased predatory impact of jellyfish over zooplankton. The jellyfish biomass increases only for 0.15 mgC m-3 at its highest compared to run 2 but it does cause deterioration of anchovy group and zooplankton.

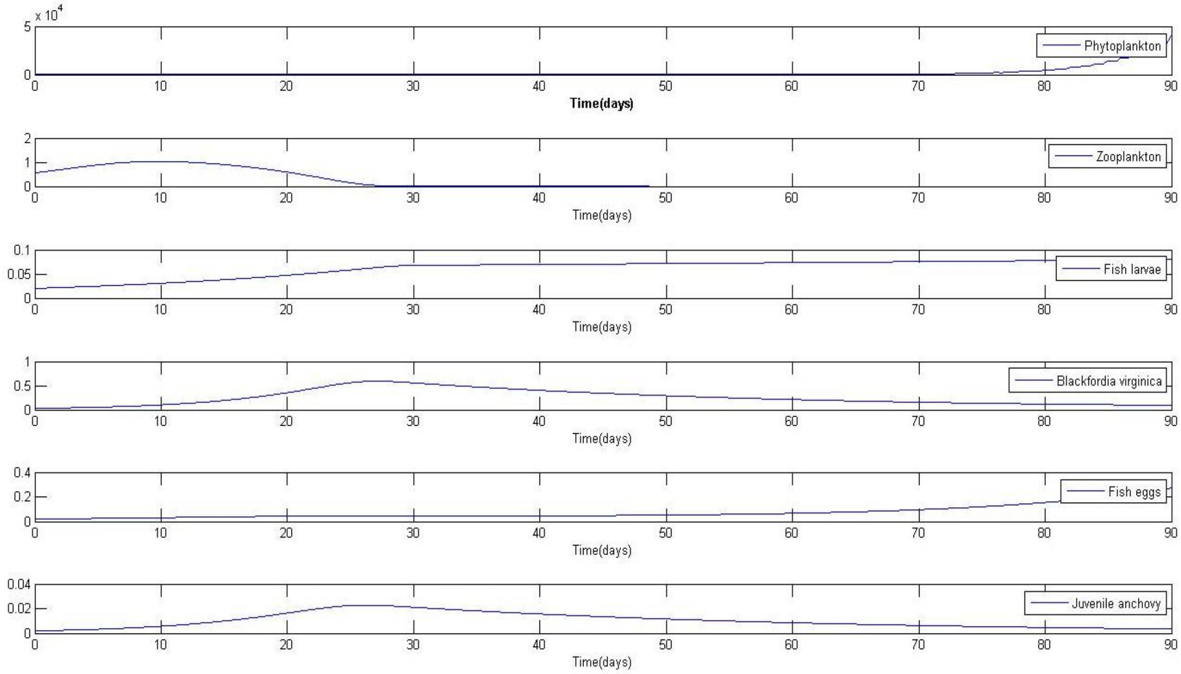

Figure 19- Biomass production of phytoplankton (mgC m-3), zooplankton, fish larvae, *B. virginica*, fish eggs and juvenile anchovy (mgC m-3) through time series of 90 days in summer conditions and nutrients availability by run 3.

4. Run 4 have some conditions as run 2 (BN =0.0015 µmol m-3, SSC=0.00002 mg m-3- low nutrient conditions) with no presence of *Blackorida virginica*.

Situation in run 4 presents a significant impact *of B. virginica* on the whole ecosystem in the low nutrient situation. All state variables are less impacted in case of jellyfish absence (Fig. 20). Phytoplankton biomass levels stay on average of 0.9- 0.01 mgC m-3 with increase up to 4mgC m-3. Zooplankton biomass decreases only in 2/3 of the summer time. Fish eggs gradually increase up to 4 mgC m-3 by the end of the summer compared to 1.2 mgC m-3 in run 2. Fish larvae and anchovy do gain more of biomass compared to run 2.

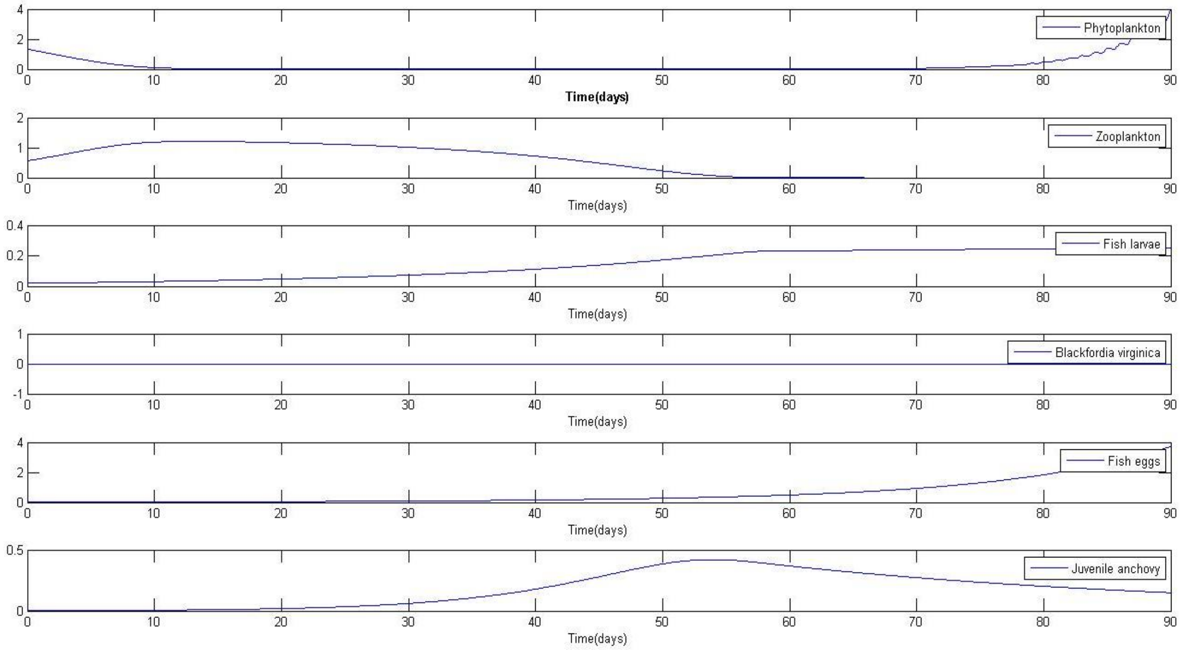

Figure 20- Biomass production of phytoplankton (mgC m-3), zooplankton, fish larvae, *B. virginica* (where biomass is 0), fish eggs and juvenile anchovy (mgC m-3) through time series of 90 days in summer conditions and nutrients availability by run

5. Run 5, before dam, Q (summer discharge) 38 m3 s-1, BN =0.6 µmol m-3, SSC=0.32 mg m-3

There is a noticeable difference in groups of phytoplankton, zooplankton, *B. virginica* and fish eggs compared to situations with low water discharge, low nutrient concentration (Fig. 20). Trend of this groups tend to change in different nutrient conditions. Significant changes in biomass content are noticed between all groups. The phytoplankton biomass in the beginning of the summer is high up to 3.3 mgC m-3 which drops and stays on the insufficient level for the whole summer (Fig. 21). Highest measured values of phytoplankton biomass in this type of conditions were up to 15 mgC m-3 though the range does correlate to the measured values before the Alqueva dam situation. Zooplankton does become predominant group in the system by the middle of the summer with up to 7 mgC m-3 which correspond to 18000 ind. m-3 (Fig. 25). Juvenile anchovy biomass grows up to 1.3 mgC m-3 by the end of the summer (Fig. 23) which results in 10 fold increase compared to low nutrient condition. *B. virginica* seems to have a large effect on all groups in the system as they do prey upon a wide variety of prey their biomass does differ in 1, 2 and 5th run (Fig. 22). The *B. virginica* highest biomass achieved is 2.5 mgC m-3 and it is highly correlated to the decrease of fish eggs biomass and zooplankton. Variations of predation rates of jellyfish for all the prey groups do result in great biomass changes. The total detritus presented as total dead organic material (Fig. 24) experiences two high contributions in the beginning from the phytoplankton and in the middle of the run from *B. virginica*. The comparison between low and high nutrient content results in increased detritus production ranging from 0.01-0.1mgC m-3 in high nutrient condition compared to low nutrient where average contribution was 0.005 mgC m-3. The initial force to run the model is seston (SSC) which in this case results in 0.32 mgC m-3 and corresponds to the similar result values of detritus. The percentage of detritus that is transferred out of this ecosystem remains unknown. Compared to low nutrient concentration simulations in this case all state variables have an initial increase and only due to the predatory effect the decrease of certain groups occur.

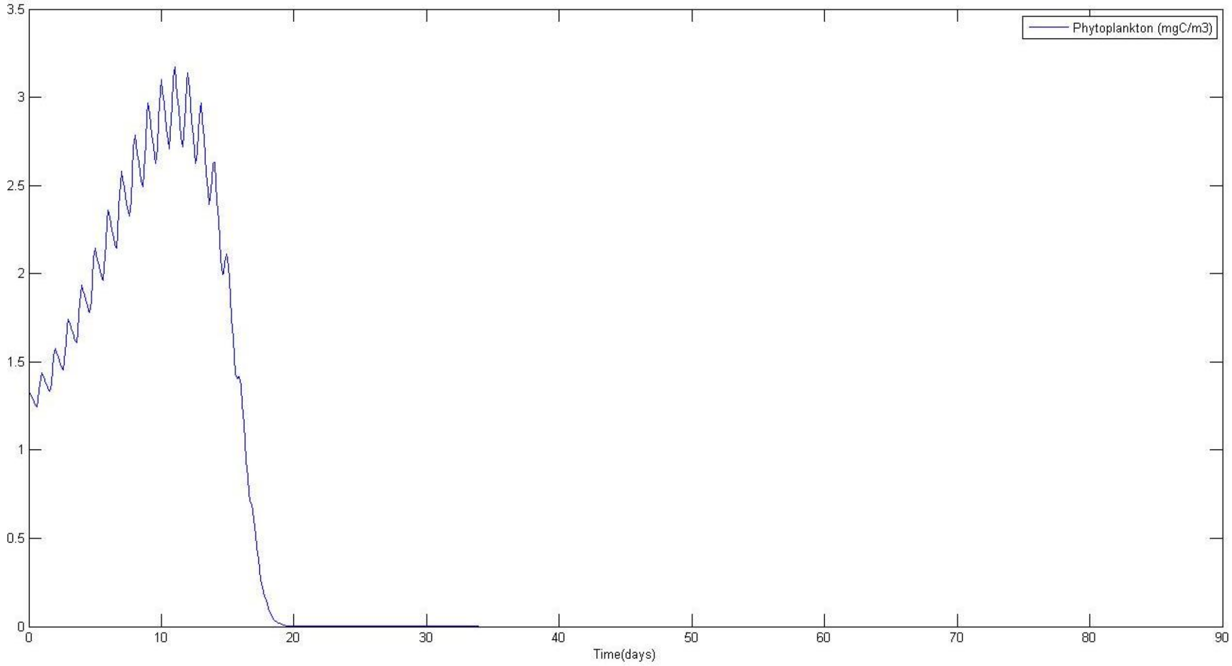

Figure 21- Biomass variation of phtyoplankton (mgC m-3) through time series of 90 days in summer conditions and nutrients availability by run 5.

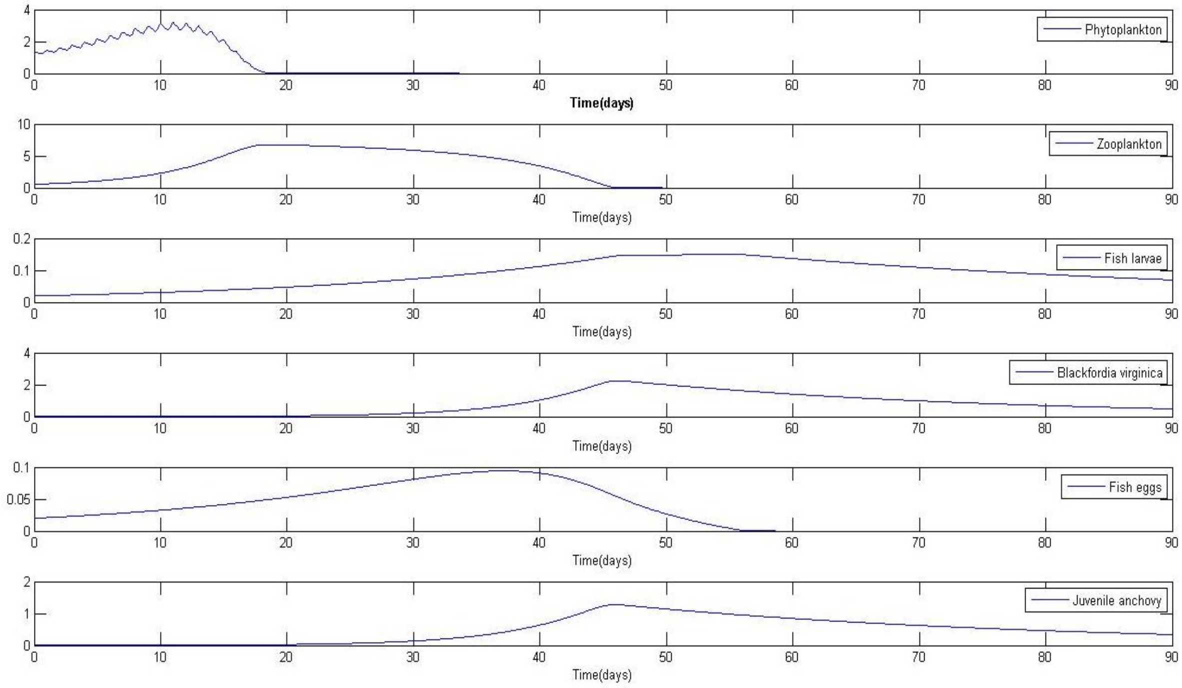

Figure 22- Biomass variation of phytoplankton (mgC m-3), zooplankton, fish larvae, *B. virginica*, fish eggs and juvenile anchovy (mgC m-3) through time series of 90 days in summer conditions and nutrients availability by run 5.

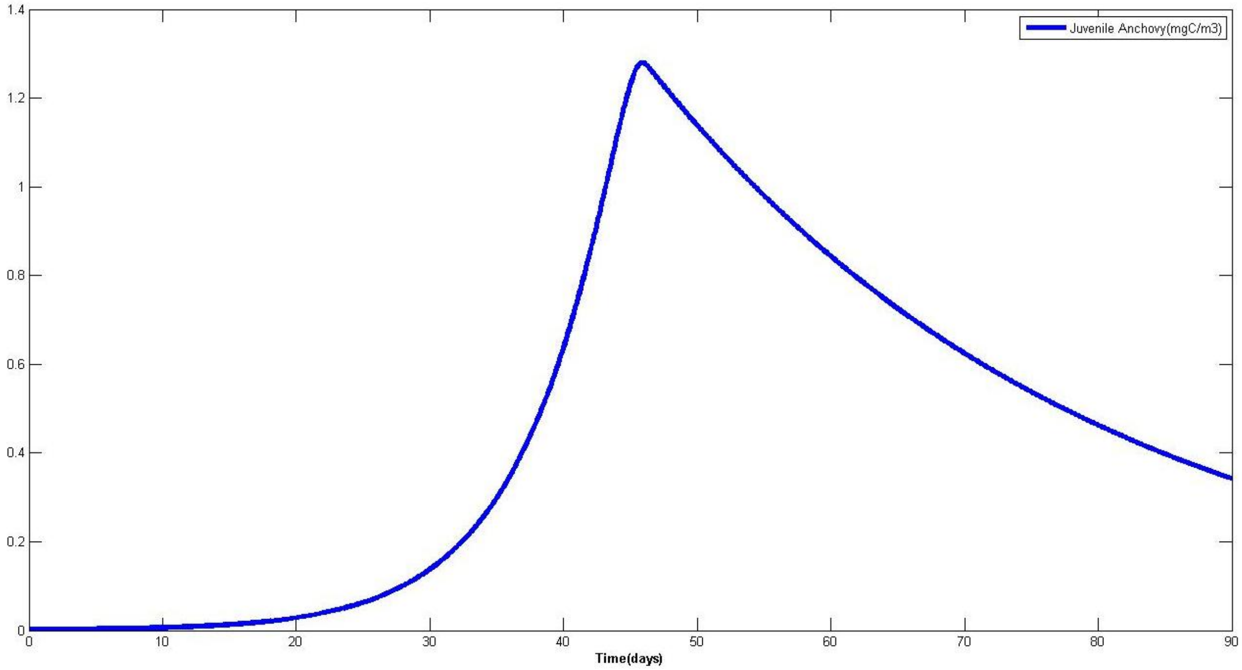

Figure 23- Biomass variation of juvenile anchovy *Engraulis encrasiocolus* (mgC m-3) through time series of 90 days in summer conditions and nutrients availability by run 5.

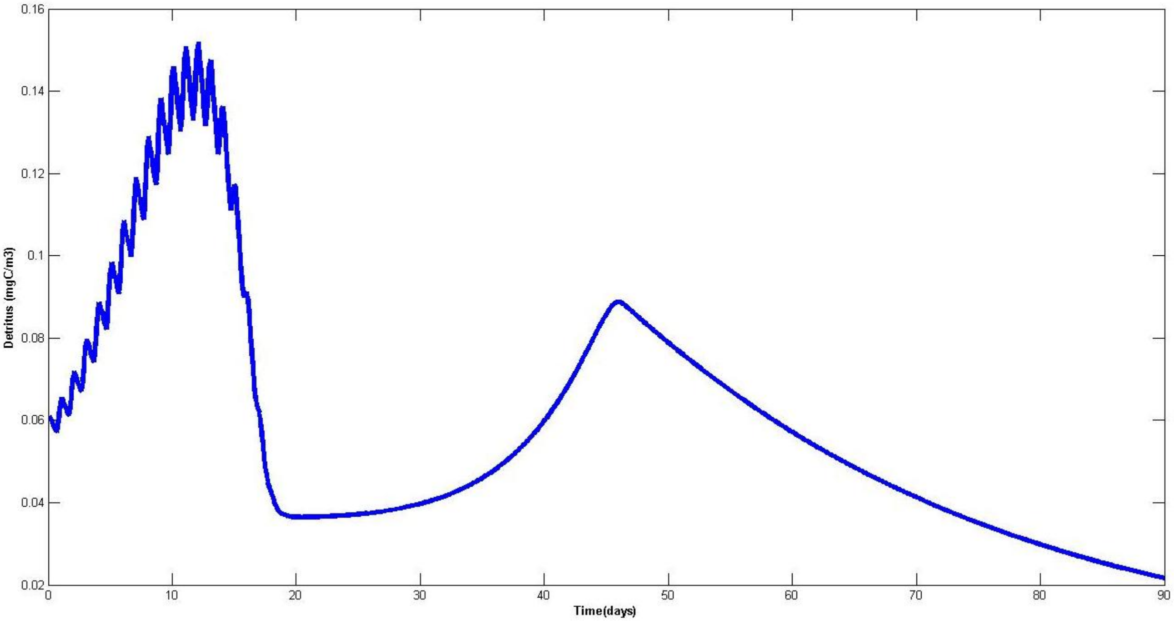

Figure 24- Total detritus production (mgC m-3) jointly together by all state variables in through summer time by conditions in run 5.

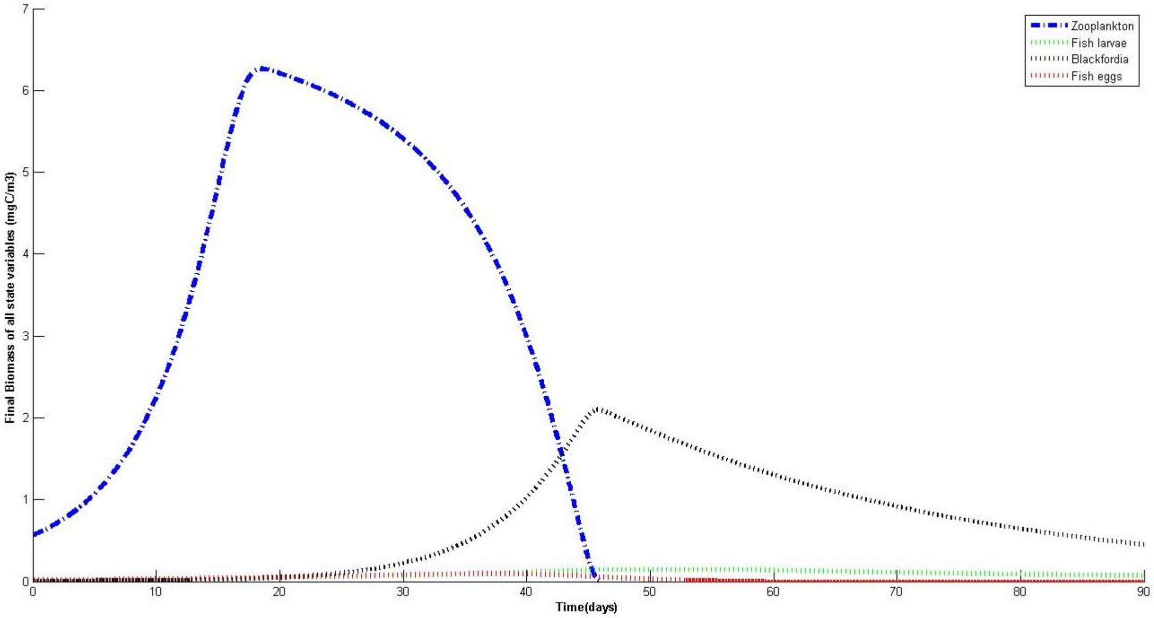

Figure 25- Biomass variation of organic carbon (mgC m-3) of each individual group in the model over period of 90 days under conditions of 5 run.

6. Run 6, before dam, Q (summer discharge) 15 m3/s, BN =0.009 µmol m-3, SSC=0.0145 mg m-3

Amount of seston (SSC) is decreased for 30 folds in this simulation compared to run 5. This variation has caused significant decrease in zooplankton groups up to half of its maximum in previous run 5 (Fig. 26). Average phytoplankton biomass has dropped down to 5* 10^-4 mgC m-3 through the run. For more than half there is a decrease in biomass of juvenile anchovy, *B. virginica* and fish eggs compared to run 5. Fish larvae group appears to be the most resistant towards changes in nutrient concentration. Detritus production from each individual group corresponds to the decrease in their biomass production (Fig. 27). Highest contribution comes from phytoplankton, zooplankton and *B. virginica* corresponding to the highest levels in time of their highest biomass. The predominant groups over the summer period are zooplankton and *B. virginica* (Fig. 28).

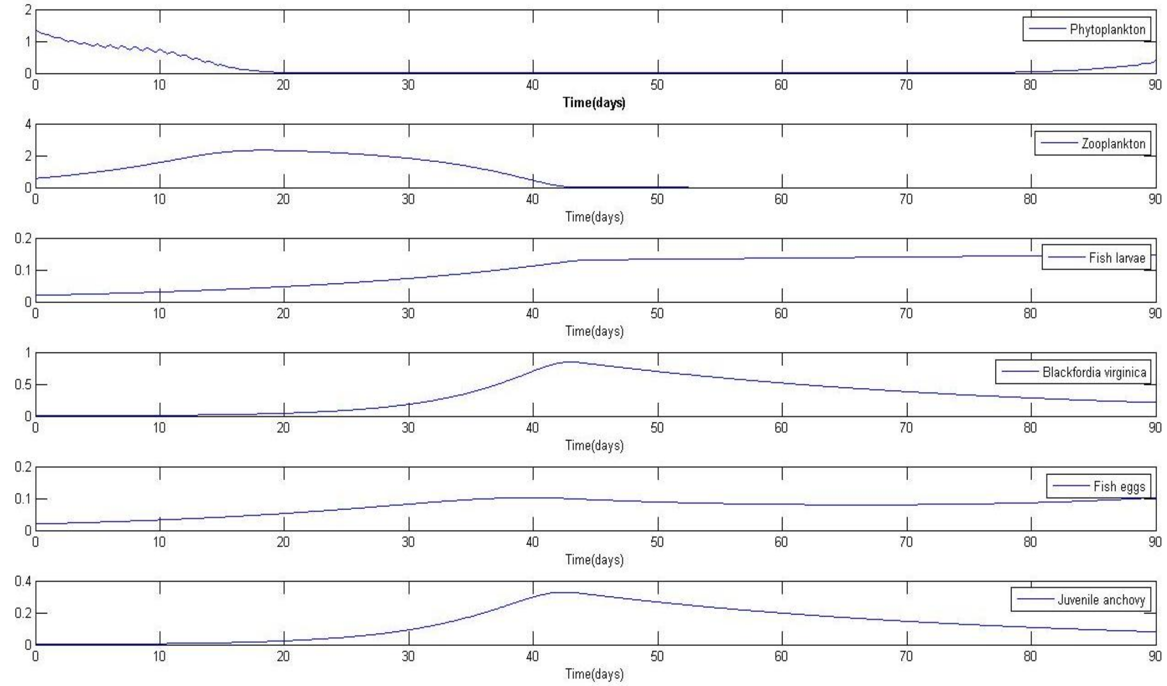

Figure 26- Biomass production of phytoplankton (mgC m-3), zooplankton, fish larvae, *B. virginica*, fish eggs and juvenile anchovy (mgC m-3) through time series of 90 days in summer conditions and nutrients availability by run 6.

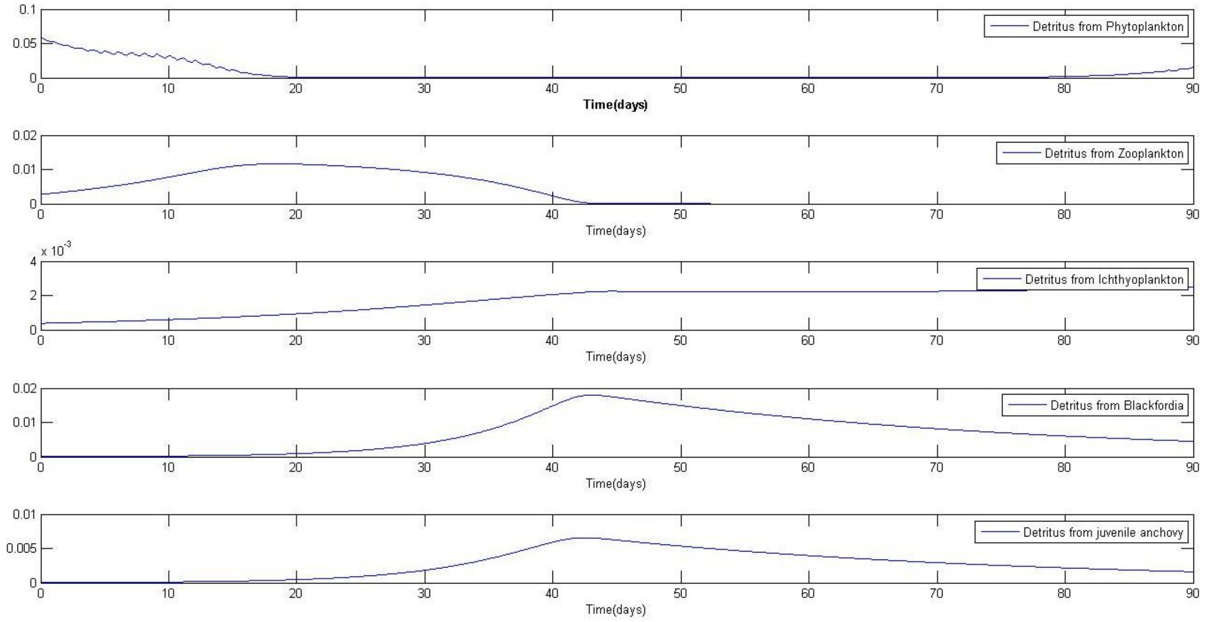

Figure 27- Detritus production of phytoplankton (mgC m-3), zooplankton, ichthyoplankton (fish larvae and fish eggs), *B. virginica* and juvenile anchovy (mgC m-3) through time series of 90 days in summer conditions and nutrients availability by run 6.

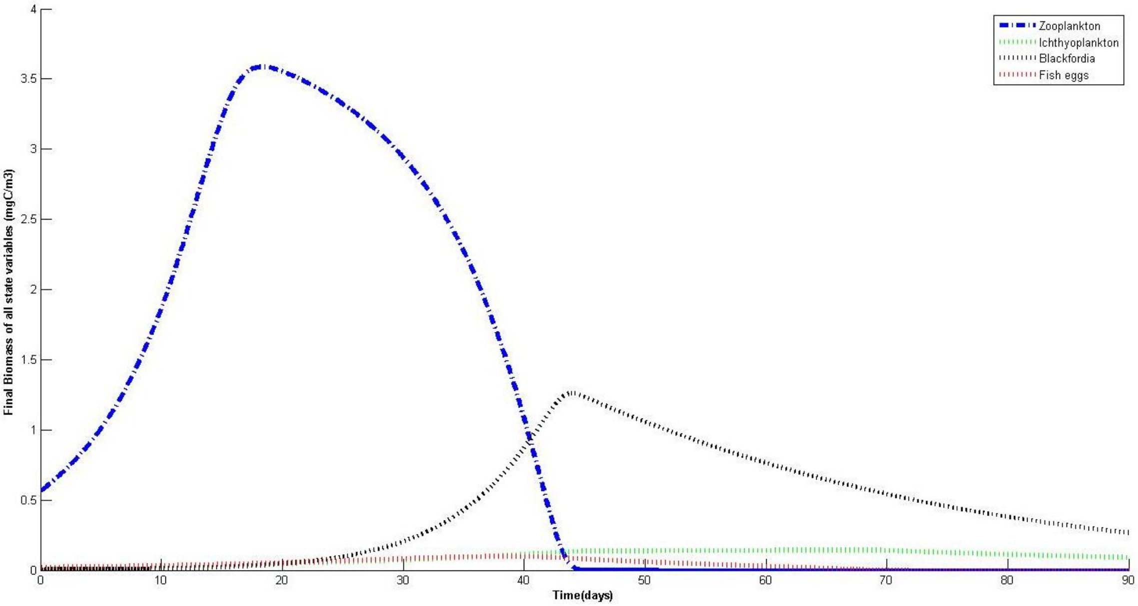

Figure 28- Biomass variation of zooplankton, fish larvae, *B. virginica* and fish eggs (mgC m-3) through time series of 90 days in summer conditions and nutrients availability by run 6.

7. Run 7 have some conditions as run 6 (BN =0.009 µmol m-3, SSC=0.0145 mg m-3) but there is an increase in initial levels of *B. virginica* from 0.003 to 0.03 mgC m-3.

In case of higher initial level of *B. virginica* biomass increased by 10 times in 7th run the zooplankton group decreases for half of its previous biomass and fish eggs are over-predated by the middle of summer. Fish larvae biomass tends to decrease by the end of the summer down to 0.03 mgC m-3 (Fig. 29). Juvenile anchovy only gain low levels of their biomass up to 0.1 mgC m-3 the highest. Initial higher level of jellyfish biomass does seem to favorize their predominance over the whole food web. Though the initial values are higher the biomass of jellyfish over the summer is lower compared to run 6 due to over- predation.

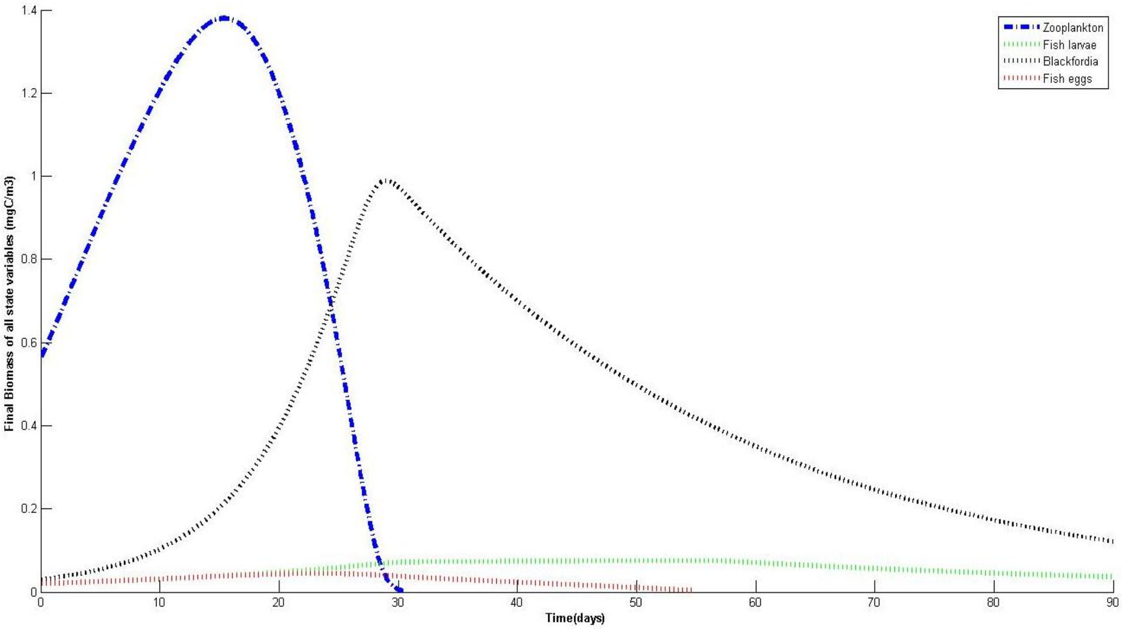

Figure 29- Biomass variation of zooplankton, fish larvae, *B. virginica* and fish eggs (mgC m-3) through time series of 90 days in summer conditions and nutrients availability by run 7.

8. Run 8 have some conditions as run 4 (BN =0.009 µmol m-3, SSC=0.0145 mg m-3) only with *B. virginica* biomass=0.

Sensitivity analysis in high nutrient conditions without presence of *B. virginica* results in increased biomass of directly influenced group of fish eggs and fish larvae and in indirectly affected group of juvenile anchovy compared to run 6 (Fig 30, 31, 32). The zooplankton group does not differ from run 6 as in this case of no jellyfish predation there is a higher predation of other predators. The phytoplankton group does not seem to differ greatly as it is controlled by zooplankton. Phytoplankton biomass does not experience high rates of decrease as it does in tests with low nutrient amount but it fluctuates on a day and night basis on a small scale of 10^-4 mgC m-3 per daily cycle through majority of the summer. Zooplankton biomass remains low through whole summer (starting from 2*10^-3 up to 10^-7 mgC m-3) and in correspondent to that there is no high increase in juveniles' biomass (Fig. 27). Juvenile anchovy achieve almost the some potential as they do in conditions of run 5 in situation with no jellyfish (Fig. 32). Fish eggs appear to be the most important group contributing to the highest biomass of the system by the end of the summer, though majority of their biomass is transferred into fish larvae biomass.

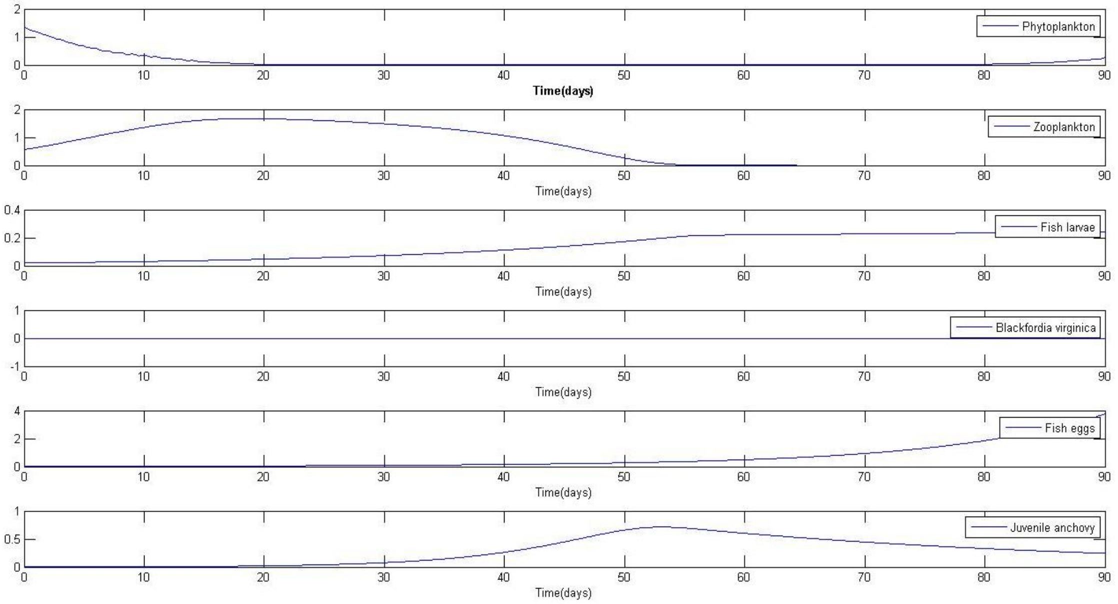

Figure 30- Biomass production of phytoplankton (mgC m-3), zooplankton, fish larvae, *B. virginica*, fish eggs and juvenile anchovy (mgC m-3) through time series of 90 days in summer conditions and nutrients availability by run 8.

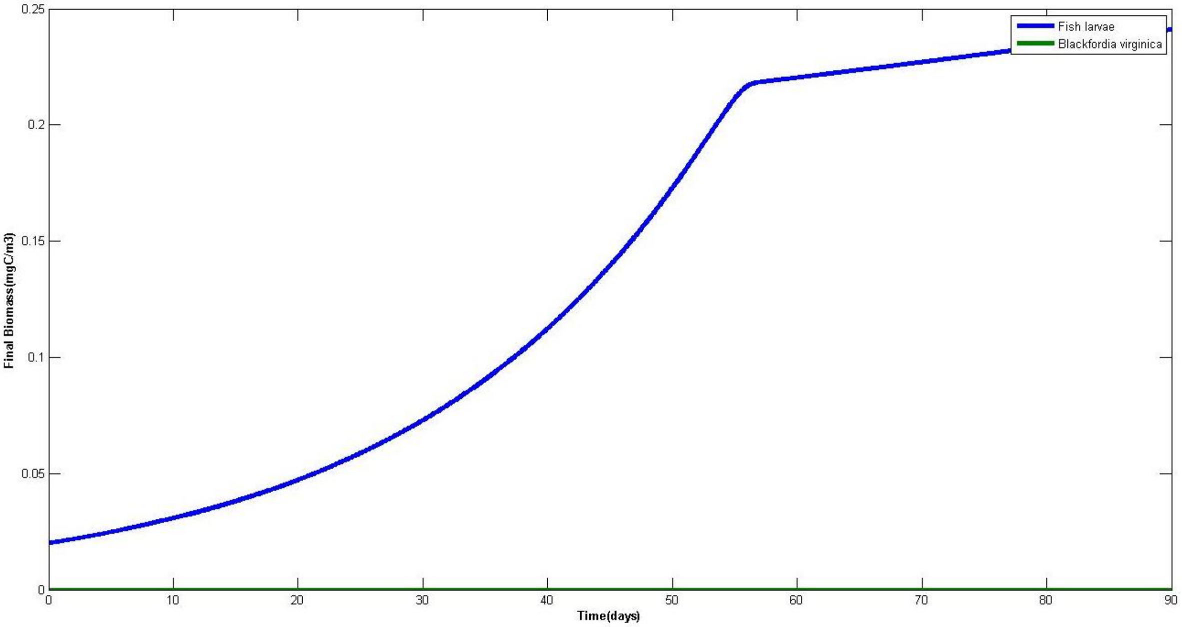

Figure 31- Biomass variation of fish larvae and *B. virginica* (mgC m-3) through time series of 90 days in summer conditions and nutrients availability by run 8.

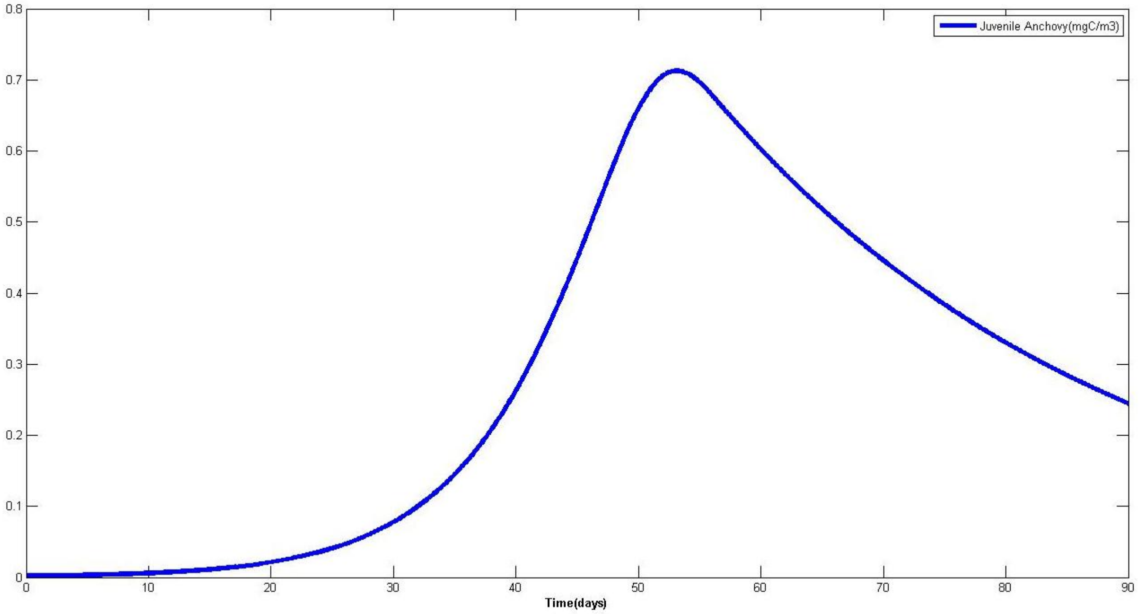

Figure 32- Biomass variation of juvenile anchovy (mgC m-3) through time series of 90 days in summer conditions and nutrients availability by run 8.

Discussion

Model of food- web dynamics including the predation impact of jellyfish *B. virginica* is proven to be realistic and simple to identify and modify each state variables parameters and coefficients. The main driven force in the model is the amount of nutrient concentration and organic matter available for the phytoplankton growth at the start of the food web. This seems to be the most influential trigger for the majority of the food web dynamics. Sensitivity analysis has proven that the phytoplankton, zooplankton and juvenile anchovy are the most sensitive organisms in the whole food web influenced by nutrient availability and water discharge. *B. virginica,* fish eggs and fish larvae biomass has proven to vary upon these conditions tested in different runs though they are not affected directly.

Situation with low water discharge and high nutrient amount appears to be the most devastating for the estuarine ecosystem. Although the sensitivity runs presented in results are always related to the combination of high water discharge/low nutrient content or the opposite a combination of high nutrient/ low water discharge could be very much realistic in case of additional nutrient loading from agricultural activities. As with high water discharge in runs 5, 6, 7 and 8 we do not enforce the flushing effect of the river current but we see it as a one way trail only for the nutrient contribution this model runs represents what would have happened in case that the nutrient level would be high and none of the produced biomass would be removed out of the system. Stating in other words the results of all state variables biomass in sensitivity testes with high nutrient concentration do seem to be a bit overestimated since the flushing effect is not incorporated in the model. This situation appeared in the first run where the average detritus production is for 10-100 folds higher compared to measured one. In this type of situation the difference between the measured and the values in the model gives us an approximate idea of how much of the solid material is transferred out of the estuarine ecosystem.

First run represents a scenario corresponding to the situation after the dam was built with low average summer water discharge of 7.5 m3 s-1 and to an average in the winter time, the most crucial time for the kick start of the whole dynamic in annually food web which was 37.9 m3 s-1 with positive NAO index (0.72) and extremely low nutrient availability (nitrate) together with solid organic material. As water discharge is very low there are no side effects on jellyfish transfer out of the estuary as there is no flushing impact. When we altered the model to impose decrease in the water discharge (run 2; 2.75 m3 s-1) in the driest ever recorded summer average the biomass of all state variables did not differ significantly from the previous run 1 except for the most impacted group of phytoplankton where there was a noticeable decrease only in the end of summer. Opposing to that fifth run represents a scenario corresponding to the situation before the dam was built with high average summer water discharge and high annual variability of water discharges (average 823.2 m3 s-1) where NAO index was negative (-3.78) and nutrient availability (nitrate) together with solid organic material was the highest recorded from year 1997. This does present upper most limits of this ecosystem that was confronted by now within the time zone of our research. Although these results are correlated to the pre- dam situation they can present a situation after the dam. Similar amount of nutrients and SSC did occur after Alqueva when the NAO index was extremely low (-1.9) which results in similar model as presented in run 6. The results from 5rd, 6th, 7th and 8th run do correspond to another situation where an increased additional nutrient loading as for instance from agricultural sources despite low river discharge could appear. The difference between these two situations is flushing effect that is present in case of high water discharge and where increased mobility of nutrients, seston or detritus occurs. Related to that in case of low water discharge over summer period as presented in run 3 in case of higher initial levels of jellyfish biomass this situation favors phytoplankton increases up to 4.5* 10^4 mgC m-3 by the end of the summer. As zooplankton is being over- predated there is no control over the phytoplankton bloom in the end of the summer. In case of run 7 where there is higher nutrient amount and some initial increase of jellyfish as in run 3 the phytoplankton does increase by the end of the summer up to 35 mgC m-3 but it is nowhere near the increase in run 3 due to higher initial rise of zooplankton which in the end is sufficient to control the phytoplankton bloom. Further on in 5 sensitivity analyses there is a clear relation between *B. virginica* and phytoplankton. Group of phytoplankton seems to be the most influential on jellyfish growth through the connection of zooplankton. There is a strong correlation of *B. virginica* increase due to predational effect over zooplankton which levels seem to be detrimental for the fish eggs. Fish larvae group appears to be the most resistant group for the *B. virginica* pressures on the ecosystem in run 5. Though the fish eggs biomass disappears by middle of the run the percentage of their biomass that was transferred into the fish larvae group tends to survive as the predation pressure of jellyfish decreases.

The jellyfish group seems to avoid collapse in biomass as they are not easily affected by the changes in the model and do prey upon a wide selection. It has been previously determinate that the increase in the jellyfish population appears to be both a symptom of the cumulative deterioration of ecosystems and the outcome of combined climate and anthropogenic stressors (Richardson *et al*., 2009). The biomass variations of *B. virginica* in tests with high or low nutrient content in the model do seem to be related to statistical analysis. *B. virginica* biomass has decreased in years with higher average annual or summer water discharge by statistics which does not directly represent the nutrient amount. In the model the water discharge is presented only through nutrient amount though the situation appears different to the one in statistics but it is certain that the jellyfish increases in case of higher nutrient concentration. We must not forget that the flushing effect is not presented in the model which could contribute to the density of *B. virginica*. Their swimming abilities might not be as strong to avoid strong currents as fish larvae can. It could be that the flushing effect would result in even higher decrease of jellyfish abundance. In the final sampling year of 2011 the density of *B. virginica* was low (below 1.3 ind. m-3) and it was found only at the mouth of the estuary. At this some year there was a negative NAO and annual water discharge was similar to the amounts before the dam was built. Statistically there is a strong correlation between movement of brackish zone and *B. virginica's* highest densities through years noticed by varieties of water discharge and intrusion of salt water upstream in years when water discharge remains low through summer. *B. virginica* newly presence in the estuary does effect biomass of ichthyoplankton. By predation they do contribute to the decrease of ichthyoplankton's biomass. Despite that they do not seem to affect zooplankton biomass majorly in case of low ichtyoplankton initial biomass when both groups fish eggs and fish larvae initial biomass is below 0.0002 mgC m-3. As *B. virginica's* biomass initial rise depends not only on zooplankton but on the amount of other prey, ichthyoplankton as well. In case of higher ichthyoplankton initial presence jellyfish biomass does not decrease but remains stable over the summer. Higher amount of jellyfish biomass through summer is responsible for the decrease in zooplankton abundance. In case of higher initial ichthyoplankton biomass levels the effect over zooplankton group seems to be increased as overall increase in their biomass affects increase in predation on a wider scale. High initial levels of zooplankton or fish eggs seem to be the most favorable for the jellyfish. The opposite can be stated for fish eggs where despite of their higher initial biomass most of it is under threat of predation. In the model fish eggs group is not directly dependent on the amount of nutrient though the triggering factor for the adult fish (anchovy or sardine) to come to spawn into the estuary is the amount of detritus taken out of the mouth of the estuary which was researched by Chicharo et al. (2001b). This means that higher levels of nutrients and detritus correspond to higher levels of initial fish eggs biomass. This correlation is responsible for increased biomass of jellyfish in the estuary. The situation with high amount of fish eggs seems plausible in case of high nutrient. High nutrient amount before the spawning period seems to favor the *B. virginica* biomass which means that years with higher precipitation through winter with possible negative NAO index favors their increased presence. Though this trend seems to oppose theory on flushing effect of jellyfish, but in the model we had proven the preference of jellyfish higher abundance over years with higher nutrient concentration. As previously mentioned flushing impact must not be neglected. Despite that we must not forget that jellyfish species use their swimming abilities to find places with higher food presence, locations with higher fish eggs abundance as they are easy type of prey. The most important two trophic levels impact interaction are relation between the phytoplankton and *B.viriginica*. Due to increased *B. virginica* biomass there is a decrease in zooplankton which regulates phytoplankton population. In situation where the zooplankton almost diminishes causes phytoplankton growth presented through multiple runs.

Knowing that *B. virginica* are not consumers on selective basis diet pattern used in a model could be extensionally different depending on type of food presence on a case to case basis. By changing their predation effort on all prey species they seem to modify biomass of prey and their own. As statistically looking there was a strong positive correlation between zooplankton biomass and water discharge and negative correlation to *B. virginica* biomass. Model has proven some trend with high nutrient amount during high levels of water discharge being responsible for the increase of zooplankton biomass. As *B. virginica* seems to be dependent on changes in available nutrient concentration they seem to be present in any type of situation and increase their biomass to substantial levels up to 2.5 mgC m-3 which correspond to extreme high to 4000 ind. m-3 not yet detected densities so far. The maximum density for *B. virginica* in other invaded systems was 232 medusae m-3 (Schroeter, 2008), 10.6 medusae m-3 in the Babitonga estuary of southern Brazil (Bardi et al., 2009), 29.5 medusae m _3 from the Rio de la Plata estuary in Argentina-Uruguay (Genzano et al., 2006), 31.70 medusae m-3 in the Guadiana Estuary of Portugal/Spain (Chícharo et al., 2009b), 66.6 medusae m-3 in the Mira Estuary of Portugal (Moore, 1987) and, 420 medusae m-3 in the Bombay Harbor-Thana and Basse in Creek estuarine complex of India (Santhakumari et al. 1997, reviewed by Wintzer et al., 2013). As density of *B. virginica* in Guadiana is low compared to other systems it means that in seasons yet to come with possible increased temperatures the density could rise significantly. With potential increase of their biomass (initial biomass was raised from 0.003 up to 0.03 mgC m-3 in low and high nutrient condition) biomass of *B. virginica* did not increase through the summer. Though in run 7 the initial values are higher the biomass of jellyfish over the summer is lower compared to run 6 due to over-predation of its prey.

B. virginica occurrence and their food source abundance were tested to identify any significant pattern in correlation to the Northern Atlantic Oscillation (NAO). The NAO index was incorporated into a model through a water discharge values measured for each individual sampling year, where the amount of water release is a direct consequence of the amount of precipitation at different values of NAO index. The model approach was used to evaluate different water discharges regimes and correlate recorded annual, summer and winter water discharge with the patterns in abundance and species compositions of prey- newly introduced predator's relation. As pulses of freshwater discharges (and their nutrients) stimulate the development of a more diversified phytoplankton assemblage that supports zooplankton (Rey et al., 1991), this is, top-down control, it does hinder harmful algae blooms (Wolanski, 2004). By the results in the model we can see that the NAO index can reflect a pattern of each individual biomass group in the food web as it is partially responsible for the nutrient concentration in the estuary. It has a direct impact on the phytoplankton and indirect on the fish egg abundance which does affect the zooplankton abundance through rise and fall in jellyfish abundance. The estuarine ecosystem does seem to be controlled from the bottom rather than experiencing top down control despite presence of new predatory jellyfish group. When there is low annual average summer water discharge appears a relative stability of the water column, which is largely driven by atmospheric forcing, is a condition favorable to jellyfish outbreaks because it permits better survival and higher reproduction of jellyfish (CIESM, 2001). Same pattern was noticed by NAO. Same pattern was noticed since 1958 from the continuous plankton recorder in the central North Sea that jellyfish is positively related to the North Atlantic Oscillation (NAO) and Atlantic inflow to the northern North Sea (Attrill et al., 2007). The biomass of jellyfish in the model does change enormously through variations in water discharge variations besides that variation in annual precipitation rate could influence the polyp survival rate through drop in temperature. Linkages to climate variation suggest that jellyfish abundance could rise and fall with ocean basinwide climate oscillations (El Niño Southern Oscillation, North Atlantic Oscillation, North Pacific Decadal Oscillation) (Anderson et al., 1999; Ottersen et al., 2001; Raskoff, 2001; Lynam et al., 2004, 2005; Purcell et al., 2005a, reviewed by Purcell, 2005b). Gibbons et al. (2009) found that at North Atlantic Ocean, seasonal and interannual variability on jellyfish peaks can be related with peaks in phyto- and zooplankton and with temperature changes. In fact, salinity and runoff were also the environmental factors which presented higher interannual variability of jellyfish in the Mondego estuary (Primo, 2012), in close proximity to the Guadiana Estuary.

In case that that there would be higher external nutrient input the phytoplankton biomass would be much higher which could result in eutrophication in case of jellyfish presence. Statistically looking through series of measuring Chl a concentration in Guadiana there is a strong positive correlation between high density of *B. virginica* and high levels of phytoplankton, stating that additional nutrients would result in phytoplankton predominance joint in community of jellyfish species. With different model runs increasing the seston and nitrogen concentration up to acceptable levels per m3 the phytoplankton biomass can differ greatly and ends up in high increase by the end of the summer. There is no linear increase of water discharge and nutrients so none of the results can be easily evaluated. We must not forget the allochthonus increase of nutrients that can be case to case specific.

The diet of *B. virginica* was predisposed on the average feeding pattern by two studies (Wintzer et al., 2013, Mills et al., 1995) based on which we have predicted *B. virginica* feeding pattern. Separated calculation of each individual group instead of substitution of all zooplankton taxa consumed by *B. virginica* should provide us with almost the same total consumption/ assimilation for *B. virginica* as it is in this case where copepods are in majority. Even within a species, diet may change simply due to an increase in size (Graham et al., 2001). Knowing that copepods (order of Calanoida) are the most dense zooplanktonic group in the Guadiana Estuary final feeding type was recalculated on their biomass as a predominant part. Though statistically data on Calanoidas' group high abundance at the time of jellyfish presence could be misleading as this group could be the only one that was successfully avoiding their predation. It has been tested before that generally, the predation impact upon copepods by jellyfish is too low to cause populations to decline (Purcell et al., 2001, Purcell, 2003), but other zooplankton groups can be more vulnerable, lacking the refuge of small size or the escape behavior of copepods (Suchman et al., 2000, Hansson et al., 2005, Suchman et al., 2008, Ruzicka et al., 2007). Model represents low resilience of zooplankton towards *B. virginica* predation and as well high impact on the fish eggs and fish larvae group. Hansson et al. (2005) noticed that predation by *A. aurita* presents high clearance rates for the fish larvae and low potential threat towards copepoda. Jellyfish in the model are able to significantly deplete zooplankton stock as their biomass gradually increases through wide diversity of prey. High predation and possible reduction of zooplankton standing stocks has been detected in other ecosystems as well (e.g. >20% d−1; Deason, 1982, Matsakis et al., 1991, Purcell, 1992, Olesen et al., 1994, Schneider et al., 1998, Purcell et al., 2001). Riisgard et al. (2012) has noticed substantial decline by the grazing impact on zooplankton depending on high seasonal abundance of *A. aurita*. Characteristics of the prey, such as size, stage and swimming speed, also affect their encounter rates with the predators and abilities to escape (reviewed by Purcell, 1985, Bailey et al., 1989). Increased size and swimming speed would increase encounter rates with predators, but also increase escapes from the predators (Purcell et al., 2001). Diet estimated from jellyfish gut contents biases toward shell or carapace bearing prey and those prey most common in the plankton (e.g., copepods) though with *B.virginica* it has been noticed that 50% of their diet can consist from ichthyoplankton, though rough estimation highly depends on their food availability. True energetic ration of jellyfish likely includes substantial fractions of unrecognizable items such as detritus and soft microzooplankton (Colin et al., 2005) or very large and rare prey (Pitt et al., 2008, Pauly et al., 2009) which was excluded from the model. Generally it has been proven that *B. virginica* jellyfish species do not find prey on its selective basis but are fed on a variety of prey that fits into the same size group. The ability to non-selectively consume a broad prey base has probably helped *B. virginica* to successfully invade new territories (Richardson et al., 2009), such as the San Francisco Estuary (Wintzer et al., 2013) and Guadiana Estuary (Chicharo et al. 2009b). In addition to the sizes of jellyfish and prey, predation rates (prey eaten/ predator day) of eggs and larvae increase directly with prey density (Bailey et al., 1984, De Lafontaine et al., 1987, Fancett et al., 1988, Purcell et al., 1994b, Purcell et al., 2001), which was presented in the model and confirms this trend. They are preying upon a wide selection and in case that there would be decreased predation rate over one group an increased predation rate would appear in another. Overall biomass assimilation would be constant as their metabolism during summer high temperatures does not differ greatly. There is no possible scenario by looking through the model where adult jellyfish would disappear from the estuary due to biological reasons for now. The food web model suggests that during the summer, jellyfish are responsible for lowering zooplankton biomass and incorporation into their own biomass. Jellyfish biomass does experience great fluctuations in all types of environment but none of the situations seem to be detrimental.

Pattern of resistance to variations in nutrient availability is seen at ichthyoplankton group both fish eggs and larvae as fish larvae biomass does not differ greatly different runs and fish eggs is not directly related to nutrient amount though fundamentally their initial biomass is. Low biomass of fish larvae is still present by the end of the summer where majority of fish larvae transfer their biomass into juvenile stage. The fish eggs and fish larvae groups in the model do concern jointly all fish species present in the estuary as the example of juvenile stage only correlates to the European anchovy which is the reason for no further correlation between fish larvae biomass with anchovy juvenile stage. The amount of juveniles that swim out of the estuarine ecosystem by the end of the summer remains unclarified. In Guadiana Estuary *B. virginica* has been associated with a reduction of densities of all zooplanktonic organisms, including eggs of *Engraulis encrasicolus* (Chicharo et al., 2009b). Nevertheless, our results showed that stations where *B. virginica* was present had reduced densities of all zooplanktonic organisms, including eggs of European anchovy *Engraulis encrasicolus* (Linnaeus, 1758) (Chicharo et al. 2009b). According to these authors, the maximum abundance of anchovy eggs and larvae registered in 2002 (after Alqueva dam) decreased 14.5 times, relative to the maximum registered in July 1988 (before Alqueva dam), a year of moderate inflow and with higher estuarine production (Chícharo et al., 1991, Chicharo et al., 2009b).

The diets of many species of gelatinous predators include mostly copepods, cladocerans, larvaceans and meroplanktonic invertebrate larvae in different proportions depending on predator species and prey availability (summaries in Purcell, 1981a, Purcell et al., 1988, Mills, 1995, Arai, 1997, Purcell, 1997), and overlap with the diets of zooplanktivorous fish, such as anchovies, herrings and sardines (Purcell et al., 2001). Jellyfish predation on zooplankton may have more of an impact on ecosystem structure and energy flow than does predation on fish eggs and larvae (Ruzicka et al., 2007). There is definite higher threat towards fish larvae as their pressure is not only predational one but they compete for the some type of prey. Juvenile anchovy do not feed on jellyfish so as jellyfish are preyed upon by few species, jellyfish could be a trophic dead-end (Ruzicka et al., 2007) and what is left from dead organic matter can only provide a very narrow selection of food for detritivores. Detritus production from each individual group results in a similar trend to the living biomass of each group. As the detritivours food web is not present in the model we have simply imported the recycling of the material back to the available food source for phytoplankton as seston (solid organic material) component in the bottom of the food web. Seston presents important concentration of nutrients at the bottom of the food web thus imposes significant differences in the whole food web, concluding that the detritus production is an important component within the estuarine food web.

The potential for competition for zooplankton prey among fish and jellyfish is very difficult to assess (Purcell et al., 2001). Whether competition would occur depends on the extent of the spatial, depth and temporal co-occurrence of the various species, as well as their consumption rates of zooplankton, and the production rates of the zooplankton (Purcell et al., 2001). In addition, demonstrating competition would require evidence that prey populations are limited by predation (Purcell et al., 2001). Direct competition between fish larvae and *B. virginica* is estimated in low and high nutrient conditions where sensitivity analysis of similar conditions with or without jellyfish presents a significant difference in the biomass of all state variables. There is a significant decrease of zooplankton in case of higher fish eggs initial biomass which gives higher predatory effect to *B. virginica*. In a model where there *B. virginica* is absent compared to the model with direct competition over zooplankton between fish larvae and *B. virginica* the fish larvae biomass does not differ greatly (for 0.1 mgC m-3). Different preterm conditions in the estuary do result in different impact levels regarding competition. There is a definite decrease in fish larvae biomass over the years of *B. virginica* presence. These potential effects of jellyfish on fish have been reviewed previously (Purcell, 1985, Bailey et al., 1989, Purcell et al., 2001, Purcell et al., 2007). If larval fish are consuming less prey due to competitive effects with gelatinous zooplankton, they may then be even more likely to fall to predation, also by gelatinous zooplankton (Wintzer et al., 2013). On the other hand the long term effect could be that the collapse of the sardine stocks lowers the predation pressure on jellyfish which increases their available food resources (Richardson et al., 2009). This possible feedback loop related to the interaction between ichthyoplankton and jellyfish, with zooplankton as a mediator could diverse the biomass growth of each group which was as well noticed by (Hong et al., 2008). Most of the interactions with jellyfish species are detrimental to fish populations, such as predation on pelagic eggs and larvae of fish, the potential competition for prey among pelagic coelenterates and fish larvae and zooplanktivorous fish species, and pelagic coelenterates serving as intermediate hosts for fish parasites (Purcell et al., 2001). There are as well other interactions which are positive for fish, such as predation by fish on gelatinous species and commensal associations among fish and pelagic coelenterates (Purcell et al., 2001). Predatory effect of fish species over *B. virginica* in this estuary were not found yet. An exception of strong top–down control was found by (Pauly et al., 2009) which involves predation by one functional group of jellyfish on another, which of course generates an apparent negative impact of jellyfish on itself. This type of control was not found in the Guadiana Estuary because the presence of other jellyfish groups such as

Aurelia aurita was never found simultaneously and as for *Catostylus tagi* the lack of information regarding this species presence was not yet sufficient to evaluate its impact on *B. virginica*. Another jellyfish *Maeotias marginata* was present in the some bloom as *B. virginica* but there was an obvious domination by *B. virginica* comparing their biomasses. Data are lacking to evaluate the magnitude and dietary importance of fish predation on pelagic coelenterates, or whether young fish of some species are dependent on medusae for survival (Purcell et al., 2001). Ruzicka et al. (2012) has proven that jellyfish had the smallest reach, i.e., jellyfish contributed the least to the production of other groups which brings up the importance of jellyfish as both trophic dead-end and production-loss pathways though they consumed the greater proportion of system production via combined direct and indirect pathways.

In case that this model would be used for different type of jellyfish species it should be modified by all relevant indicators used in a model as for instance; predation rate, bell diameter, clearance rate, prey type composition, growth rate, assimilation rate. To assume that all jellyfish have the same diet and exist at the same trophic level would be very wrong (Pauly et al., 2009). Indeed, their different morphologies, swimming modes, prey capture, and nematocyst composition yield widely different diets (Purcell et al., 1988, Costello et al., 1995, Peach et al., 2005). Thorough investigations into jellyfish population dynamics require long term data sets, and these data are not uniformly distributed worldwide (Condon et al., 2013, Hay, 2006). This is especially true in estuaries, where jellyfish can be intermediate-top level predators (Baird et al., 1989, Condon et al., 2008, Kaneshiro, 2013) or it can become difficult to assess their competition and predatory impact.

The relationships between fish and jellyfish in this case are as well of particular interest due to commercial important species of fish in the estuary as are *Engraulis carniolus* and *Sardina pilchardus*. The anchovy biomass representation could be correlated to sardine biomass in the model as they feed and grow in similar rang. Massive presence of jellyfish can reduce the possibility of catching fish, deteriorate the quality of fished organisms and increase costs, due to increased fuel use, thereby reducing the income of fishermen and, eventually even threatening their employment (Nastav et al., 2013). Another factor that could impact the expansion of jellyfish species is when over fishing includes fish species such as anchovies, herring and sardines, there could be significant unconsumed zooplankton, and pelagic coelenterate populations might expand (Caddy, 1993). In spite of the lack of quantitative data on predation rates, there are instances where overfishing of a predator is believed to have contributed to increases of pelagic coelenterate populations (Purcell et al., 2001). With the reduction of zooplankton they impose fish decline due to lack of prey as presented in all runs in the model. The predational impact of *B. virginica* over zooplankton strongly affects biomass of juvenile anchovy. In at least one other upwelling system, the Benguela Current off Namibia, jellyfish had displaced the once abundant planktivores (sardines and anchovies) causing major ecosystem changes (Lynam et al., 2006, Utne-Palm et al., 2010).

Detritus production over period of 90 days contributes up to 0.05-0.15 mgC depending on initial nutrient concentration and it derives out of all exudation and mortality rates of presented groups. The highest contribution of 8 mgC m-3 to total detritus was due to increased phytoplankton by the end of the summer. In case of high rate of phytoplankton growth the majority of detritus is their contribution though in this case large amount of detritus triggers a self- control system over phytoplankton as the light penetration is limited and turbidity limits the overall phytoplankton growth. Feeding rate of jellyfish on the decaying substance is not included in the model as well. Decay time of organic matter depends on the composition of each individual species, its age and size. Decay of organic matter is temperature dependent. Jellyfish decay faster than the rest at any temperature, and above 15°C, t approaches half a day. Fish decay slower than jellyfish, and only above 20°C, t approaches 1 day, phytoplankton decay much slower than the other groups, and even at 30°C, t remains above 4 days (Lebrato et al., 2011b). Gelatinous biomass turnover proceeds faster (Lebrato et al., 2011b). During summer the average temperature in Guadiana are above 20°C reaching up to 27, 7 °C which means that based on a previous preposition the remineralization of detritus produced from jellyfish would be much faster and so contribute back to the food web as part of the significant proportion of N and C required for phytoplankton growth. Higher amount of detritus would become recycled inside of the Guadiana Estuary ecosystem due to fast decay. Jellyfish- POM is widely known to be an important component in the diet of scavengers, and at certain times of the year when gelatinous biomass is available, it could be the dominant resource (Lebrato et al., 2011b). Benthic animals were observed periodically feeding on the decomposing material, thus indicating that jelly-falls have an active role in benthic food webs. This means that, apart from bacterial decomposition, large organisms (mega- and macro-fauna) also play an important role in regenerating gelatinous biomass (Lebrato et al., 2011b). The amount that is lost from the estuarine ecosystem and contributes to the coastal system is unknown and remains only as an unknown percentage of the biomass presented in the model. The biomass that is not remineralized stays at the seabed as jelly-falls and so with the increased amount of precipitation in the end of the autumn increases turbidity and higher amount of detritus is taken out of the estuary to the open ocean zone. The peak of detritus coexists with the timing of phytoplankton dye off. Under such conditions of low light penetration and high turbidity, the silica deficiency hypothesis suggests that non-siliceous phytoplankton, such as flagellates proliferate and replace diatoms (Harashima et al., 2006), resulting in a reduction in the size of primary and secondary producers (Cushing, 1989, Richardson et al., 2009). In the end this type of food web favorize jellyfish as top predators and extents their presence to late autumn. Besides that a low C/N ratio of jellyfish organic material implies a higher organic matter lability as remineralization occurs faster when nitrogen-rich compounds are present (Lebrato et al., 2011b). Excretion of dissolved organic matter may also support bacterioplankton production but few data are available (Pitt et al., 2009). The importance of decomposition of jellyfish following blooms and the contribution to benthic communities has only recently been investigated (Billet et al., 2006, Rieman et al., 2006, Titelman et al., 2006, Purcell et al., 2007).

Salinity and temperature were significant predictors of medusae abundance with moderate salinity and high temperature resulting in their highest abundance (Schroeter, 2008). According to Attrill et al. (2002) estuarine nursery grounds may act as thermal buffers against more severe open-sea conditions without being affected directly by marine conditions. It has been proven that most non- native species are well adapted to the salinities holding lowest native species richness, already in their native area, and that non- native species richness maximum in brackish water seas occurs in the salinity intervals of native species richness minimum (Paavola et al., 2005). This could lead us to misinterpretation or overestimation of predation impact of *B. virginica* in the estuarine turbidity maximum zone. As their food preference is mixed this trend was not used in the model though it was statistically proven in the Guadiana. From the model it can be only concluded that they are very effective invaders and have successfully found their own niche in the ecosystem.

Temperature in the Guadiana Estuary in summer time is stable and for jellyfish metabolism accelerating one so we did not include this factor in a model. Both low and high temperatures can disable enzymes and transport systems, which physiologically restrict organisms to their adapted temperature ranges (Kaneshiro, 2013). This would be a completely different story in an annually based model of polyp's survival rate under temperature range. Direct effects of temperature can be positive (increased strobilation rates and hence the production of young medusoids) and negative (increased mortality of the benthic polyp) (Liu et al., 2009). Medusae populations fluctuate under the simple rule of "the warmer the better", with collapses after polyp mortality in severe winters and peaks in years with mild winters and long summers (Ruiz et al., 2012).

To what extent exploitation of *B. virginica* can participate and modify the present food web. Possible range of scenarios is presented here within a model but are there any solutions to stop the over- exploitation? Mills et al. (1995) had found that it is possible to control their bloom biologically. For example, hydroid populations are often grazed by nudibranchs and it may be that a nudibranch will discover the new hydroid populations in San Francisco Bay estuaries (Mills et al., 1995). For now we have no up to date data that would correlate this predator- prey relation in Guadiana Estuary. To what extents do jellyfish affect the energy transfer Ruzicka et al. (2012) had proven that it has a more web scaling effect and less a community restructuring effect? That hypothesis does seems reasonable though we have to point out that they do present a direct effect on the biomass of other groups stating that they are able to effect the recruitment dynamics as it was noticed by (Suchman et al., 2008).

To what extent anthropogenic influence has on spreading and increasing the jellyfish biomass in the estuaries? Reports of increasing problems with jellyfish, especially in East Asia, are too recent to exclude decadal climate cycles (Purcell et al., 2007) which could mislead us to wrong conclusion that major cause in these ecosystems are jellyfish interventions. Certainly the Alqueva dam has contributed to their increase since the present conditions are in their favor. First of all their existence in this area would not be able without introduction through ballast water. There are certain prepositions that jellyfish populations are increasing. Changes in the environment are able to change the biological clock of each species and consequently on their relation on annually temporal spatial scale. Evidence shows that jellyfish abundances fluctuate with climatic cycles (Purcell et al., 2007). Occurrences of jellyfish will most likely increase over the next century as the NAO moves into a stronger positive phase in response to global warming (Osborn, 2004). Even more close relation was noticed between zooplankton density and water discharge which is main food for *B. virginica* so this could be even more important than direct influence. Some evidence suggests continued upward trends (Attrill et al., 2007); however, recent time series are still too short to exclude circa-decadal climate cycles (Purcell et al., 2007). Because of the key role planktonic copepods and gelatinous carnivores (jellyfish hereafter) play in the dynamics of marine ecosystems (Mills, 1995), it is essential to know how the year-to-year changes of these trophic groups are controlled over long time scales (Molinero et al., 2005). In a review (Purcell et al., 2007) conclude that human effects on coastal environments are certain to increase, and jellyfish blooms may increase as a consequence. The complexity of food web dynamics should be part of a long term research and seen through anthropogenic changes since records taken for each specific ecosystem. Models using jellyfish species not only as part of density in trophic networks but including their physiological, behavioral, feeding and growth capabilities should be more often used in order to predict and learn more about this important type of predators.

Conclusion

This study is unique in that that there are relatively few studies focusing on modeling of the food web dynamics approach where jellyfish species is included as individual group . The results obtained by the model developed in this thesis are in conformity with field measurements to what it concerns biomass values of each individual group in the model. Jellyfish *B. virginica* presented in the model does impact the ecosystem integrity with directly decreasing the biomass of prey and indirectly decreasing biomass of other groups of organisms through competition. *B. virginica* possesses higher threat in case of high nutrient condition and low water discharge as there are no flushing effects. What is the amount of detritus or pelagic groups that are not able to oppose to the current is transferred out of the system and what is their along- channel distribution remains unknown. Behavioral pattern correlated to jellyfish species swimming abilities and their biomass along channel distribution remains not clarified by the model. Nutrient and seston concentration appears to be the most influential trigger for the majority of the food web dynamics. Sensitivity analysis has proven that the phytoplankton, zooplankton and juvenile anchovy are the most sensitive organisms in the whole food web influenced by nutrient availability and water discharge. *B. virginica,* fish eggs and fish larvae biomass has proven to vary upon these conditions tested in different runs though they are not affected directly.

Comparing the system with or without jellyfish presence in high or low nutrient environment the results prove that jellyfish do possess control over the whole ecosystem. The most impacted group by *B. virginica* is zooplankton which controls phytoplankton growth from top down. These relation causes bottom up control as zooplankton biomass influences the ichthyoplankton and juvenile anchovy biomass. In case of high winter water discharge the detritus production is higher and the turbidity at the mouth of the estuary attracts higher amount of adults fish to spawn. Higher fish eggs biomass causes higher and faster growth of *B. virginica* which is able to consume higher amount of zooplankton and with that controls the decrease in juvenile anchovy population and fish larvae survival rate. Possible presented scenario is over- predation of zooplankton which can lead to phytoplankton bloom. *B. virginica* increase in biomass (over 0.45 mgC m-3) is able to deplete zooplankton population and cause potential eutrophication within the estuarine zone. As they affectively prey upon the ichthyoplankton they are able to affect fisheries stock. What is the threshold level of the estuarine ecosystem and what is the level of jellyfish biomass when the ecosystem is not able to cope with changes anymore it is hard to say. In a present model we can see that the species *B. virginica* as being a non-selective predator is able to integrate into the system affectively and that it is able to decrease biomass of other organisms in the system to certain level depending on many biotic and abiotic parameters in the model.

It would be plausible to follow up jellyfish annual summer presence of adults in the estuarine ecosystem to better understands their dynamics. As the jellyfish long term presence can significantly influence the integrity of an ecosystem it is crucial to follow their dynamics and predict future changes of the system in order to adapt towards its changes. For better understanding of *B. virginica* functioning in the ecosystem it would be good to follow the polyps dynamic. Including the annually based cycles of polyps dynamics over a longer period into the model is highly recommended. It is much more effective to work on a potential threat knowing what possible impact jellyfish can have. Preterm solutions can radically change the final results of fishing depletion as it could happen in Guadiana as anywhere else within highly modified estuaries. The model presents a strong ecohydrological connection where the fluctuation in jellyfish biomass strongly as does biomass of all other organisms in the Guadiana Estuary strongly depends on the hydrological conditions over the year.

Acknowledgments

I would like to thank to Prof. Dr. Alexandra Chicharo who has been a great support to me over the last five years. My early scientific career would never be realized without her support. I would very much like to thank her for all the opportunities where I could work under her supervision and gain precious experiences for further on in the career. It is an honor for me to work with such a great person.

In a very crucial moment Dr. Radhouan Ben- Hamadou appeared and offered great help to me. Without him I would never be able to work and learn about modeling. Thank you for all the knowledge that was given to me regarding modeling. I appreciate all the working hours that were done in a really friendly environment.

I would never be even close to all the experiences and knowledge that I gained through the time of this master of Erasmus Mundus Master of Science on Ecohydrology. All the credit goes to Prof. Dr. Luis Chicharo. Thank you for giving me the possibility to participate in such a reachful experience. It was a treat.

I would never be able to climb so high without the support of my family. Thank you granny/ mum, David, Lana and Tiby for believing in me.

In the end I would like to thank to all of my friends helping me and supporting me through such a crucial time as master thesis work joint with pregnancy was. Thank you all MSc Kasia Scrozynska, Vitor Perreira, Joanna Wlodarczyk, Dorotka Szałaj and Francisco Rey for offering me help when I needed it the most.

I would like to thank to Slovene Human Resources Development and Scholarship Found for making it possible.

I would like to thank to all that have contributed their sampling data that were available for the model.

Ljubljana, 12.12.2013

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Annex:

I. Conversion rates for parameters used in the model.

Note: all conversion rates are not the exact corresponded to the calibration done by the author of the scientific paper provided. The final rate used in the model could be slightly adapted in order to fit in the model through the process of calibration.

a) Conversion to ash free dry weight (AFDW) of individual *B. virginica* was estimated from bell diameters using Wintzer's relation (Wintzer, 2013),

WWT= (2.785*10^-5)*dm^2.089;

where dm is bell diameter (mm) .

After that the carbon content for jellyfish, which is only 10%, is multiplied with ash free dry weight.

b) Predation rate of *Blackfordia virginica* for all prey type:
Zooplankton: where the average predation rate is multiplied with the dry weight and abundance with possible modification al later calibration.

Table 4-Predation rates of *B. virginica*

Average predation rate	8.8	ind./day	(Wintzer, 2013)
Average predation rate	1.4	ind./ day	(Mills et al., 1995)
Average of the reference data	5.1	ind./ day	
Predation rate based on diel composition of guts content	1.848	21% was fish larvae composition rate	(Wintzer, 2013)

Average size and type of the prey was defined by (Wintzer, 2013) and used in the equation for predatory rate.

Table 5- Prey type and size for *B. virginica* within zooplankton group.

Copepods	52%	
Copepod nauplii	45%	
Barnacle nauplii	28%	
prey size	0.25-0.7	mm

c) Conversion to ash free dry weight (AFDW) of individual zooplankton was estimated by average length of zooplankton (1.075 mm), for individual fish egg with average 1.25 mm, for individual fish larvae with average length of 5.5 mm using Bamsteadt relation (Bamsteadt, 1990),

$$\mathbf{Y(\text{mg AFDW}) = 0.000765*(\text{mm diameter})\ \wedge^{2.766}}$$