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EFF Project: Ecosystem Based Management of Irish Fisheries and other resources (CA/033766/11)

Work Package 3:

The relationship between micro-plankton and fisheries yield in the western Irish Sea

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Summary

Since the beginning of the 20th century there has been an awareness of the relationship between primary production (PP) and fisheries yield (FY) and a number of attempts have been made to derive values of the potential yield of fish from estimates of primary production. With the introduction of the Marine Strategy Frame Work Directive (MSFD) there has been renewed interest in energy flow through food webs as an indicator for the food web descriptor (D4). However, estimating fisheries yield from primary production is not a trivial task because of the complex and dynamic nature of marine food webs. In this report we present the results of a preliminary investigation of the relationship between primary production and fisheries yield in the Irish Sea. We compared literature based relationships between PP and FY with those derived more recently for the Irish Sea.

Our results suggest that when compared to empirical relationships between primary production and fish landings derived from 1980s data, the current Irish Sea catch of demersal and pelagic fish is low (0.31 kg C ha^{-1}) compared to the estimated level of gross primary production of 142 g C m^{-2} y^{-1}. Similarly, the catch is low compared to the potential yield predicted from simple trophic-dynamic equations. Chlorophyll and PP data for the Irish Sea showed little change since the early 1990s while the catch of pelagic and demersal fish has declined (and the catch of shellfish has increased). Whether the changes in landings are due to overfishing or changes in ecosystem structure and functioning requires further study. Estimates for *Nephrops* landings show that currently 31% of the available PP is required to sustain this yield.

Large uncertainties in the relationship between PP and FY make estimating yields from primary production a challenging task and simple regression models might not therefore provide a useful indicator for energy flow through the system. Other models incorporate similar uncertainties not least due to the large open boundaries of coastal marine ecosystems and the exchange of nutrients, organic material, and migratory fauna with neighbouring waters. More sophisticated models have been developed to investigate exploited aquatic ecosystems and he next step for the Irish Sea is to apply these modelling techniques to support policy and further investigate the influence of top down (fisheries) and bottom up (climate and human) pressures on Irish Sea ecosystem structure and functioning.

Rationale

In 2011, the Department of Agriculture and Rural Development (DARD) awarded a European Fisheries Fund (EFF) grant to the Agri- Food and Bioscience Institute (AFBI) to provide advice on the implementation of an ecosystem approach to the management of Irish Sea fisheries and other resources. The study was divided into four work packages: (1) to document the science and best practice relating to the implementation of an ecosystem approach to managing marine fisheries and other ecosystem services; (2) to undertake three ecosystem surveys of the Malin Shelf sea area; (3) to investigate microplankton production/ fisheries yield relationships; (4) to determine the status of the western Irish Sea micro-plankton community.

This is a report to DARD on work package 3. The key aim was to investigate microplankton production/ fisheries yield relationships. The method used was to conduct a literature review on this topic. It was further to apply a modelling approach to quantify any trends in Irish Sea microplankton production using AFBI and Cefas data (1992 to 2011). The agreed measure of success was a report to DARD (August 2013) documenting Irish Sea productivity over the last two decades and the relationship between primary production and fisheries yield.

1. Introduction

Phytoplankton is the collective name for the microscopic algae that live in the aquatic environment of our planet. Just like plants on land, the many hundreds of species that make up the phytoplankton harness sunlight to produce organic matter. This organic matter provides food for microscopic animals, small grazing animals (zooplankton) and ultimately fish, sea birds and sea mammals. Fisheries yield is therefore dependant on the phytoplankton. The production of organic matter by phytoplankton and the role played by the zooplankton in transferring the energy in this matter to other parts of the food-chain are critical to the health of marine ecosystems.

Since the beginning of the 20th century scientists have been aware of the relationship between primary production and fish production and have tried to estimate how much fish was potentially available for human use on the basis of the production from phytoplankton (Ryther, 1969). Recently, there has been renewed interest in this topic and the transfer of energy through the food web from the perspective of the European Marine Strategy Framework Directive (MSFD).

The MSFD (2008/56/EC) requires EU Member States to report on the environmental status of the seas under their jurisdiction to achieve '*Good Environmental Status'* (GES) by 2020. GES is based on meeting targets for eleven qualitative descriptors: 1. Biological diversity, 2. Non-indigenous species, 3. Population of commercial fish / shell fish, 4. Food webs, 5. Eutrophication, 6. Sea floor integrity, 7. Alteration of hydrographical conditions, 8. Contaminants, 9. Contaminants in fish and seafood for human consumption, 10. Marine litter and 11. Energy and noise. The designation of GES requires that the attributes of the ecosystem represented by each descriptor are considered to be in a 'good' state. The focus of this report is Descriptor 4 (Food webs).

Before discussing the descriptor in detail, a brief introduction is given to the concept of the marine food web and its structure and functioning. Food webs are complex networks of feeding interactions between consumers and their food. The species composition of food webs varies according to habitat and region, but the principles of energy transfer from sunlight and plants through successive trophic levels are the same.

Marine pelagic food webs in temperate waters are inherently variable but there are recurrent seasonal cycles, driven largely by the annual cycle of solar heating and cooling. At the simplest level a food web is a food chain (Fig. 1). That is a pathway of the transfer of energy and matter between feeding (trophic) levels. A food web is made up of many inter-linked food chains and can be seen as a hierarchical network of feedback loops (trophic interactions). The sum of these interactions forms an intricate web. Despite the evident general structure and linkages in food webs (e.g. energy transport from phytoplankton to zooplankton) their complexity makes it difficult to identify a single characteristic which represents good environmental status.

The classic view of a pelagic food web was that of an efficient transfer of energy via a short food chain from large diatoms to copepods to fish (Hardy, 1923). However, since the 1970s this classical view has been modified and changed. It is clear that the microbial loop (Williams et al., 1981; Azam et al., 1983,) that involves the utilization of carbon by bacteria, protozoa, and small copepods (Edwards and Burkhill, 1995) has added to the complexity of marine food webs and to the rates of inorganic and organic material flux in the oceans.

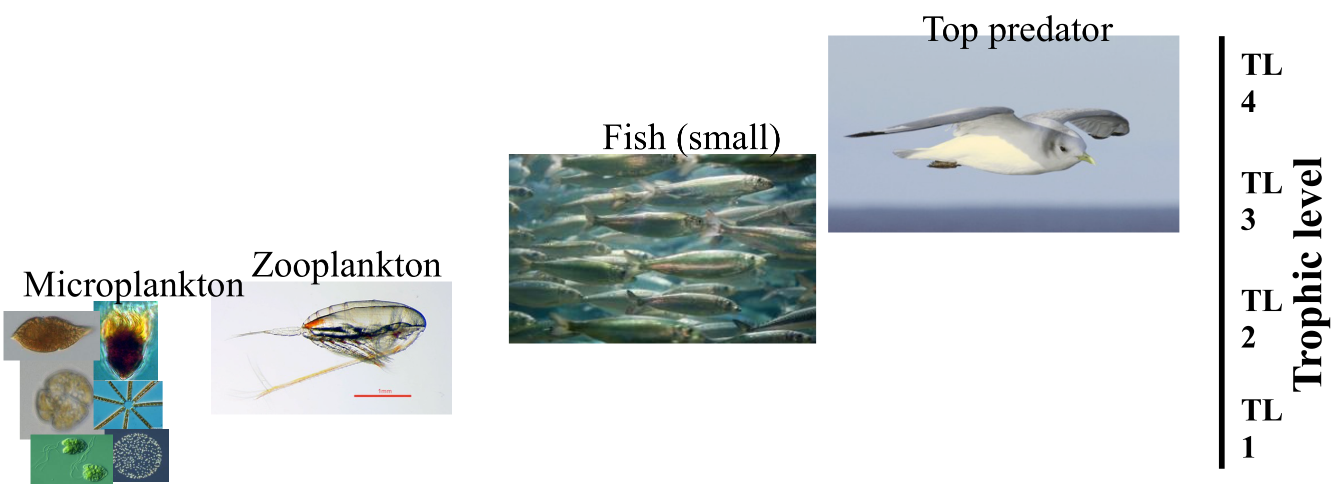

Figure 1: A simple pelagic marine food chain from microplankton via zooplankton to fish to the top predator in this case a sea bird.

Legendre and Rassoulzadegan (1996) pointed out that viewed from a fisheries perspective scientists distinguished between two pathways in the pelagic ecosystem: (i) a short, efficient pathway from large diatoms and copepods to fish (Cushing, 1989a) with a large energy export to higher trophic levels; (ii) a less efficient microbial loop pathway comprised of small phytoplankton, cyanobacteria, heterotrophic bacteria and protozoa. However, Legendre & Rassoulzadegan (1996) suggested that in reality there is a continuum of trophic pathways between these two extremes, and that various points along this continuum are characterised by specific combinations of dominant organisms and nutrient-cycling processes. The importance of these newly discovered trophic components and the understanding of interactions have led to a re-evaluation of the pathways and rates of transfer of energy in marine pelagic food webs (Fig. 2).

The MSFD food web descriptor (D4) addresses the functional aspects of marine food webs, especially the rates of energy transfer within the system and levels of productivity in key components. Good environmental status for D4 requires that:

> *"All elements of the marine food webs, to the extent that they are known, occur at normal abundance and diversity and levels capable of ensuring the long-term abundance of the species and the retention of their full reproductive capacity."*

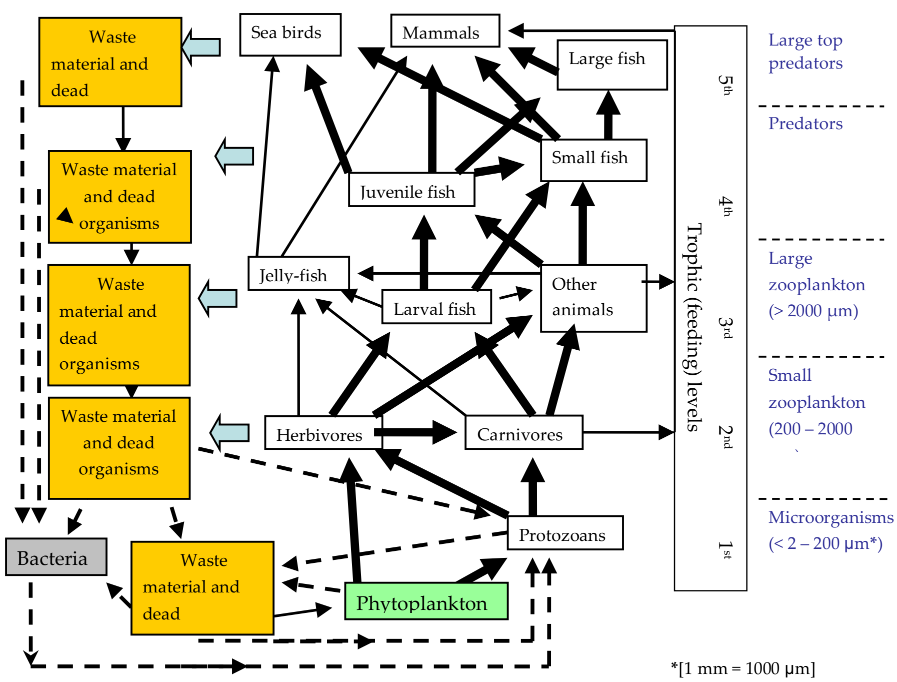

Figure 2: A complex food web with trophic levels on the right hand side.

Tett et al. (2007) considered the question of ecosystem health in relation to undesirable disturbance resulting from eutrophication. They (Tett et al., 2007) suggested that a healthy ecosystem, like a healthy human body, is a system that functions well and is able to resist or recover from disturbance. The health of an ecosystem has the quantifiable elements of *vigour,* *organization*, *resistance*, and *resilience*. Here, we consider the first two elements. The *vigour* of an ecosystem is the transfer of energy through its different biological components and its ability to recover from disturbance by means of re-colonization and population growth. The *organization* (or structure) of an ecosystem is its biodiversity and the interactions between species. GES or a healthy ecosystem therefore depends on its structure and function.

The European Commission established working groups to review indicators and targets that could be used for each of the MSFD descriptor. The food web working group (Rogers et al., 2010) identified two key attributes for D4:

- Energy flow through food webs which allows a diagnosis of the state of the system;
- Structure of food webs that is the size and abundance of organisms which are attributes and integrals to maintain predator prey relationships.

The working group also considered that there were three aspects of energy flow in food webs which were feasible to measure and could be applied at a regional scale. These are:

- ratios of production at different trophic levels;
- the productivity (production per unit biomass) of key species or groups;
- trophic relationships

In this report we present the results of a preliminary investigation into the relationship between primary production and fisheries yield in the Irish Sea. As a first step we review the scientific literature on the topic of energy transfer efficiency. The second part of the study involves the use of data from the Irish Sea to determine the productivity of the western Irish Sea and compare this with data on fish landings (catch). An additional aim was to determine whether there have been any long-term changes in phytoplankton production.

1.2 Irish Sea fisheries

The Irish Sea is located on the north western European continental shelf bounded by the land masses of Ireland and the UK. It extends from St George's Channel in the South (connecting it to the Celtic Sea) to the North Channel in the North (connecting it to the Malin Shelf). The geographical borders of the sea are taken to be between 52 N (St David's Head to Carnsore Point) and 54 40'N (Mull of Galloway). The Irish Sea is a small coastal sea with a volume of

2430km^3. The surface area is 48,200km^2 (Brander and Dickson, 1984). Details of the general oceanography of the Irish Sea are given in Scherer and Gowen 2013d (see also Gowen et al. 1995; 2002).

Although the Irish Sea is small its natural resources are of considerable economic importance. Connolly and Molloy (2000) estimated the value of fish and *Nephrops norvegicus* (Norway lobster) landings in 1998 to be £43 million. The estimated value of landings to Northern Ireland ports in 2008 was £24 million (19,529 tonnes of fish, crustaceans and shellfish) (Gibson, 2011).

1.2.1 Fishery of demersal and pelagic fish

Demersal fish live and feed on or near the bottom of the sea. There is a distinction between strictly benthic fish which rest on the sea floor and benthopelagic fish which float in the water column just above the sea floor. Examples for benthic species that are of commercial importance are flounder, sole, turbot, plaice, and halibut. Species such as cod and haddock make up the main part of the commercially fished benthopelagic fish. Demersal fish commonly feed on benthos, zooplankton, fish eggs, crustaceans and small fish which are all generally considered trophic level (TL) 2 and in the case of small fish and crustaceans TL 2.5. Demersal fish are therefore placed between TL 3 – 4.

For the demersal fishery in the Irish Sea, cod, haddock, plaice and sole are the species of commercial importance. The Irish Sea landing to ports in Northern Ireland of demersal fish in 2008 was 1,894 t and had a market value of £3.18 million (Gibson, 2011). Pelagic fish live near the sea surface or in the water column, i.e. the pelagic environment of the sea. Most pelagic fish swim in shoals that can weigh up to hundreds of tonnes. Small forage fish are able to prey on individual zooplankton (TL2) such as copepods, fish larvae and eggs and can also filter feed on phytoplankton (TL1) when this is energetically more efficient. Therefore, species such as herring and sardines are placed at TL 2.5. The large predator fish that feed on small forage fish are generally placed at TL 3.5 – 4. The main pelagic fishery in the Irish Sea is for herring and in 2008, 5,722 t were landed into ports in Northern Ireland with a market value of £1.34 million (Gibson, 2011).

1.2.2 Lobster fishery

The lobster fishery is currently the main fishery in the Irish Sea with the emphasis on *Nephrops norvegicus* (also known as the Dublin prawn). There are two important fishing grounds for *N. norvegicus* in the Irish Sea, one in the western Irish Sea (~3,504 km^2) and a second, smaller ground (~876 km^2) in the eastern Irish Sea. Assuming that the *Nephrops* population is restricted to the soft sediment (its natural habitat) regions of the Irish Sea mud patches of the seabed, the total area for the *Nephrops* fishery is 4380 km^2.

The pelagic larva of *N. norvegicus* is a component of the zooplankton community in the western Irish Sea and the development of seasonal stratification and a cyclonic gyre of near surface water, is thought to be particularly important to the recruitment of *N. norvegicus* larvae in the western Irish Sea (White et al., 1988). The gyre acts as a retention mechanism, keeping the larvae over the deep muddy trough, corresponding closely to the distribution of adults (Hill et al., 1994; Hill et al., 1996; Dickey-Collas et al., 1996). The gyre is also thought to restrict water exchange limiting the import of larvae from populations outside the western Irish Sea. Therefore recruitment to the stock is particularly dependent on local larval production and survival.

Since the decline in demersal fisheries, *Nephrops* is the most valuable and main fishery in the Irish Sea (landings to ports in Northern Ireland in 2008 were 7,876 t with a market value of £14.2 million), therefore it is important that it is fished sustainably. It is geographically isolated and there is close coupling between the physical environment and plankton dynamics (Smith, 1987; Tuck, 1993). *Nephrops* larvae feed mainly on zooplankton at trophic level 2 of the food web and are therefore placed at TL3.

2. Literature review

2.1 The relationship between primary production and fisheries yield

Fisheries management has long been interested in attempting to estimate future harvests and how much fish is potentially available for human consumption. Schaeffer (1965) suggested that one method was to estimate the energy transfer through the food chain (Figure 3) from primary production.

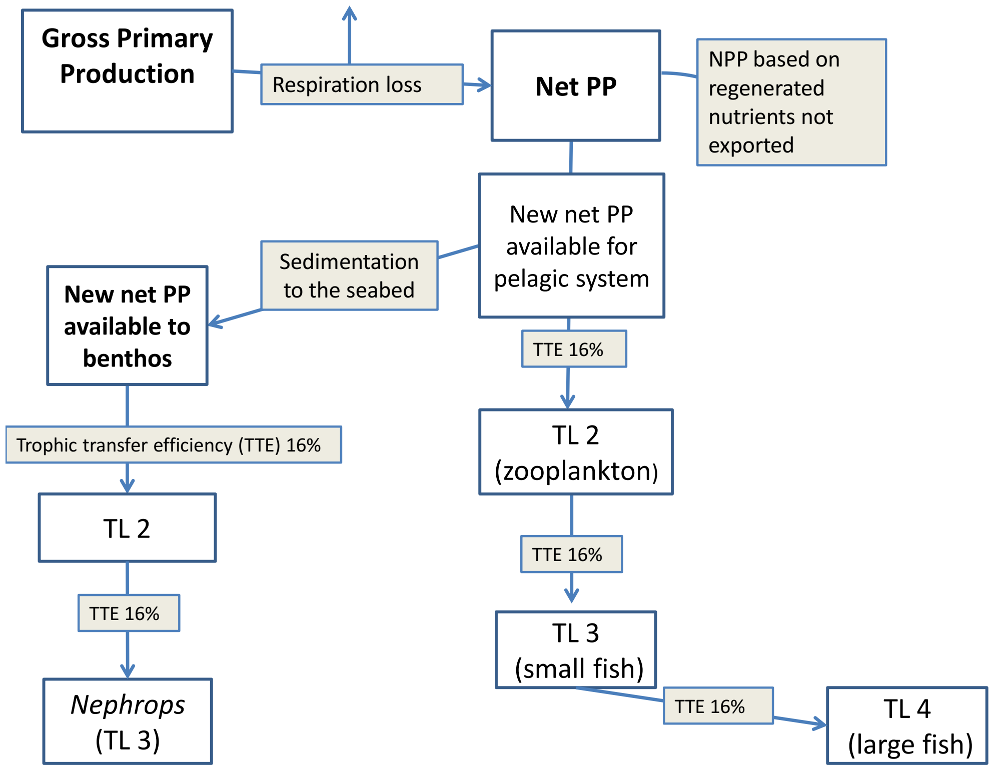

Figure 3: Flow diagram of a simple energy budget from primary production to pelagic and demersal fish (right) and *Nephrops* (left).

A key question when considering energy flow through a food web is the efficiency with which it is transferred through the food web. As Schaeffer (1965) pointed out, increasing the efficiency of transfer will increase the yield at a given trophic level. Parsons et al. (1977) defined ecological efficiency (E) as the following:

$$E = \frac{Amount\ of\ energy\ extracted\ from\ a\ trophic\ level}{Amount\ of\ energy\ supplied\ to\ a\ trophic\ level} \quad (1)$$

According to Slobodkin (1961) and others (see Pauly and Christensen, 1995) the value of E is on average 10%. However, Parsons et al. (1977) pointed out that it is important to know how correct this value is because it can greatly influence the final estimates of production. Barnes and Hughes, (1999) reported a transfer efficiency of 20% from phytoplankton to the herbivore level and Pauly and Christensen (1995) stated that efficiency can vary between 2 and 24% depending on the availability of food and the growth rate of organisms. Ryther (1969) considered efficiency to be 30% in young, actively growing organisms. Hill (2007) gave an estimate of 27% for the efficiency of energy transfer between primary production and herbivorous zooplankton (TL 2) during the 2004 spring bloom in the western Irish Sea.

Mullin and Brooks (1970) gave an even higher value (30 to 45%) for the energy transfer from primary production to benthic herbivores. As an overall estimate, Parsons et al. (1977) proposed an energy transfer to the herbivore level of no less than 20% and efficiency for all higher trophic levels of between 10 and 15%. Based on the above we used a value of 16% for each trophic level.

Carbon (C) is used as a common "currency" because Gibbs free-energy content of organic matter is mostly held in C bonds. Therefore energy transfer is often approximated by C transfer in trophic-dynamic model calculations that explore factors affecting marine fish production (Iverson, 1990 and references cited therein).

2.2 Studies in freshwater

There have been a number of attempts to relate fish yield to primary production in freshwater. Malack (1976) and Oglesby (1977) were amongst the first to develop empirical relationships between fish yield and phytoplankton production and biomass. Malack (1976) developed a regression equation that expressed fish yield as a function of gross primary production and Oglesby (1977) developed an empirical relationship based on a simple linear regression of fish yield against phytoplankton standing stock (as measured by chlorophyll) using data from 19 large (surface area > $10km^2$) lakes. The regression equation was:

$$\log Y_f = - 1.92 + 1.17 \log CHL_s;\ n = 19;\ r2 = 0.84 \qquad (2)$$

where Y_f = annual yield of fish, expressed as dry weight per square metre of lake surface; CHL_s = summer standing stock

Oglesby (1977) suggested that an approximate conversion of Malack's annual production estimates to comparable ^{14}C uptake rates gave a reasonable fit to an extrapolation of the regression Oglesby established for smaller lakes (Area < $10km^2$). However, Machena and Fair (1986) found that the models of Malack (1976) and Oglesby (1977) gave contrasting results when applied to two different lakes in which the yield was largely of the same species. Other empirical relationships have been derived between measures of primary production and fish production (Jones & Hoyer 1982; McConnell et al., 1977; Liang et al., 1981). A global analysis of the relationship between freshwater fish production (PF; kg ha^{-1} yr^{-1}) and primary production (PP; g C m^{-2} yr^{-1}) by Downing et al. (1990) gave the general relationship:

$$\log_{10} PF = 0.600 + 0.575 \log_{10} PP \qquad (3)$$

The correlation coefficient was 0.79. Fish production was also significantly correlated with mean total phosphorus concentration ($r^2 = 0.67$). These authors suggested that the conversion of phytoplankton into fish production was dependent on lake trophic status with oligotrophic lakes being ~x100 more efficient than hyper-eutrophic lakes but less productive overall.

2.3 Studies in marine waters

According to Ryther (1969): *"numerous attempts have been made to estimate the production in the sea of fish and other organisms of existing or potential food value to man".* Ryther (1969) was one of the first to publish his work on using a simple trophic-dynamics model (after Schaeffer, 1965) to relate global annual primary production (ACP) to fisheries production (FP).

$$FP = ACP \times E_1^n \times c_1 \qquad (4)$$

Where: FP = fish production (g wet wt m^{-2} y^{-1}); ACP = Annual Carbon Production (g C m^{-2} y^{-1}) by phytoplankton; E_1 = C transfer efficiency; n = number of trophic transfers; c_1 = constant of the ratio of fish wet to dry weight (3.3) and the ratio of dry weight to C (2.4) = 7.9.

Ryther (1969) assumed a transfer efficiency of 15% for coastal zones and offshore areas of high productivity and estimated a potential global annual fish production of 120 million t wet weight at trophic level (TL) 3.

Nixon (1988) compiled data on landings (fisheries yield, FY) and primary production from 36 marine systems and found that yield was significantly related to primary production (Fig. 4). The equation of the fitted line was:

$$FY = 1.55 \ln PP - 4.49 \qquad (5)$$

Using a similar approach (Fig. 4) Iverson (1990) usd a sub-set of Nixon's data from ecosystems with phytoplankton based (pelagic) food webs. His analysis gave the regression equation for the relationship between landings (fish catch, FC) and phytoplankton production (ACP):

$$FC = -0.80 + 0.024 \times ACP \qquad (6)$$

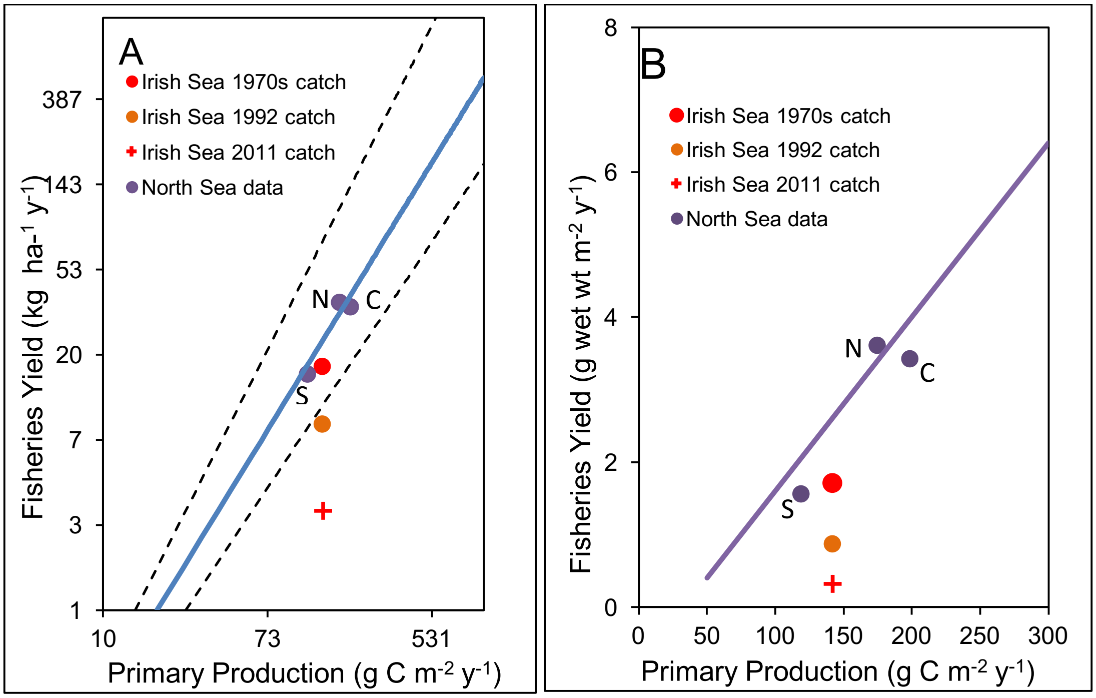

Figure 4: Estimates of fisheries yield from the Irish Sea and North Sea derived from the Nixon regression equation (A) and the Iverson regression equation (B). The dashed lines in A, encompass all of the 36 data sets that were used by Nixon (1988) to calculate the regression equation. N, C and S are northern, central and southern North Sea data respectively.

Iverson (1990) found that of the datasets investigated, on average the catch was 25% of predicted fish production (Fig. 5) which is similar to the value given by Ryther (1969).

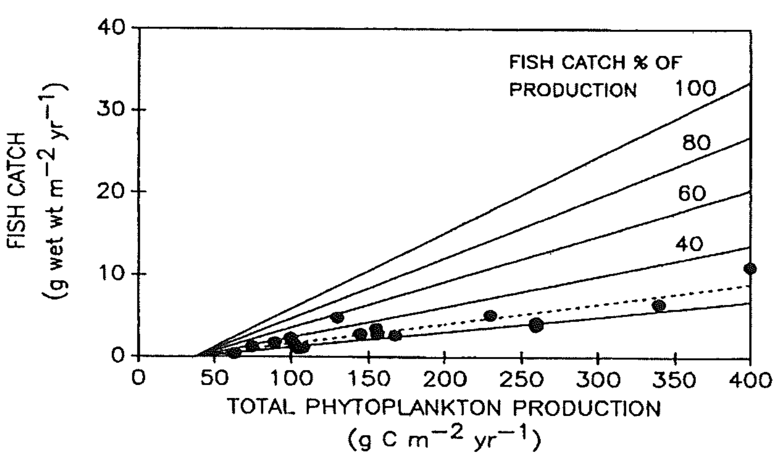

Figure 5: Fish catch as a function of total phytoplankton production from Iverson (1990). The data were compiled by Nixon (1988). The dashed line represents a linear regression equation fit to the data (see Eq. 7).

More recently, Ware and Thomson (2005) investigated the relationship between satellite derived surface chlorophyll (as a proxy for primary production) and fish yield in coastal waters of the NW of the United States and Canada. Interestingly, these workers recognised the difficulty posed by migratory species when trying to relate primary production to yield and only considered the yield of resident fishes. Ware and Thompson (2005) found a significant linear relationship (Fig. 6) between chlorophyll and fish yield which was consistent over large and smaller (10,000 km^2) geographical areas, and concluded that: "*long-term average fish production and yield within large-scale fishing zones along the continental margin of western North America are mainly controlled by phytoplankton production.*"

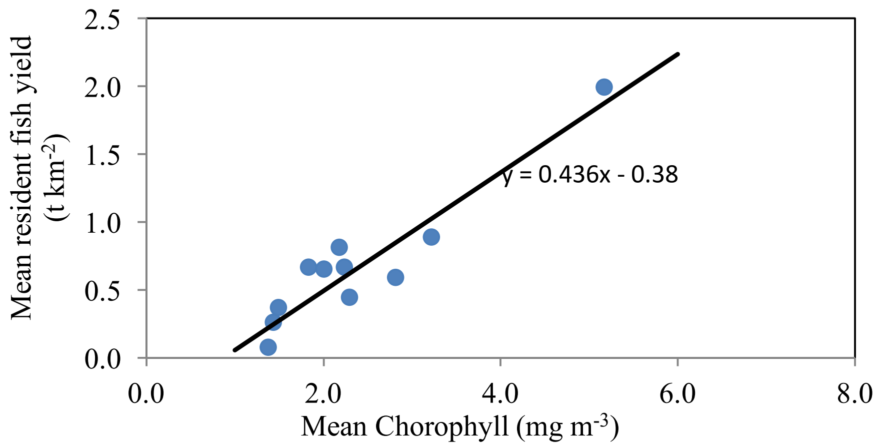

Figure 6: The relationship between satellite derived annual mean surface chlorophyll (mg m^{-3}) and the mean yield of resident fish (t km^{-2}) in western shelf waters of North America. (From Ware and Thompson, 2005).

3. Methods

Details of the methods for measuring chlorophyll concentration and estimating carbon fixation (primary production) by phytoplankton are given by Gowen et al. (1995) and Capuzzo (2011). The seasonal pattern of biomass and gross primary production was modelled using a 'harmonic' or Fourier time-series method (Capuzzo 2011). The 1992 and 1993 biomass and production data of Gowen et al. (1995) were used with a Montecarlo method (use of random numbers) to generate a synthetic data set to determine the 90% confidence limits around the seasonal cycle and generate a median value for annual production with 90% confidence interval.

Fisheries data have been taken from the report of the ICES Working Group for the Celtic Seas Ecoregion (Division VIIa) (ICES 2012). For the purposes of this report the term '*catch*' is used for the yield of fish and shellfish including discards (where the data are available).

Inclusion of discard data is important because the discard/ bycatch can behigh for some species. For example, large amounts of demersal fish (mostly young fish) are caught and discarded by the *Nephrops* fleet. The catch also includes migratory fish such as herring that migrate in summer to feed on the Malin shelf but reproduce in the Irish Sea. Finally, the data do not include non-commercial species (sprat etc.) some of which are present in large biomass.

4. Results

4.1 Chlorophyll standing stock and primary production in the Irish Sea

The seasonal cycle of chlorophyll standing stock derived from the Fourier time-series analysis of the 1992 and 1993 data from the AFBI mooring site in the western Irish Sea shows a peak in spring with a second smaller peak in late summer (Fig. 7). Data from more recent years generally fall within the boundaries of the 5 and 95%ile of the model which define the seasonal envelope of variability. The majority of the chlorophyll data points outside these confidence limits are from 1999 and 2000 but there is no indication that the onset and duration (phenology) of the seasonal cycle of biomass has changed over the last 20 years.

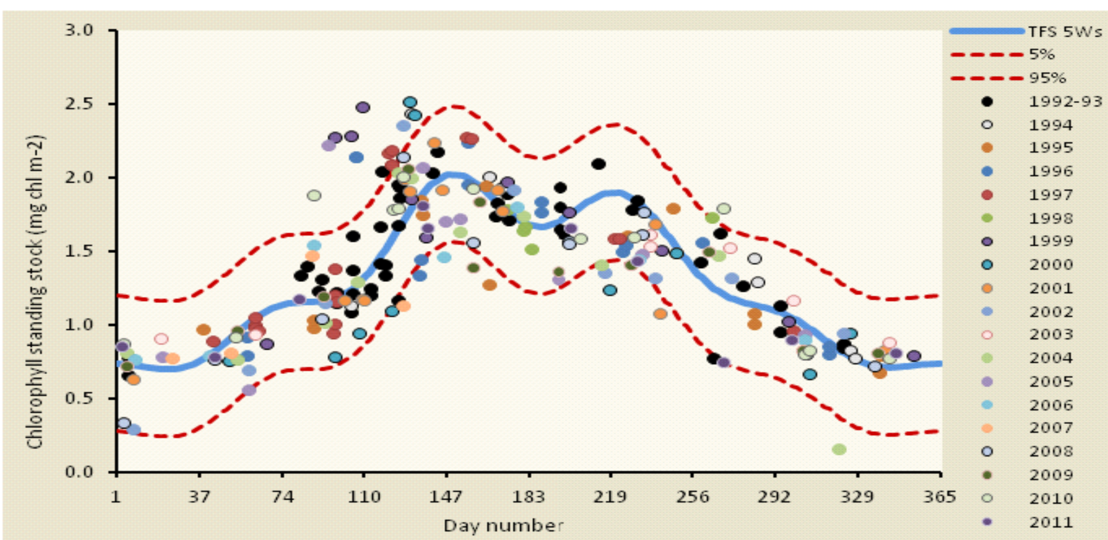

Figure 7: The annual cycle of chlorophyll standing stock in the seasonal stratified offshore region (station 38A) of the western Irish Sea over the last 20 years.

The modelled seasonal cycle of gross daily production (Fig. 8) is similar to that of chlorophyll standing stock. The graph also shows that the 2010 and 2011 estimates of gross daily production were within the 1992 - 1993 seasonal envelope of variability. Based on all of the primary production data, the median value of annual gross production in the seasonally stratifying region of the western Irish Sea is 204 g C m^{-2} y^{-1} with a range from 157 to 291 g C m^{-2} y^{-1}.

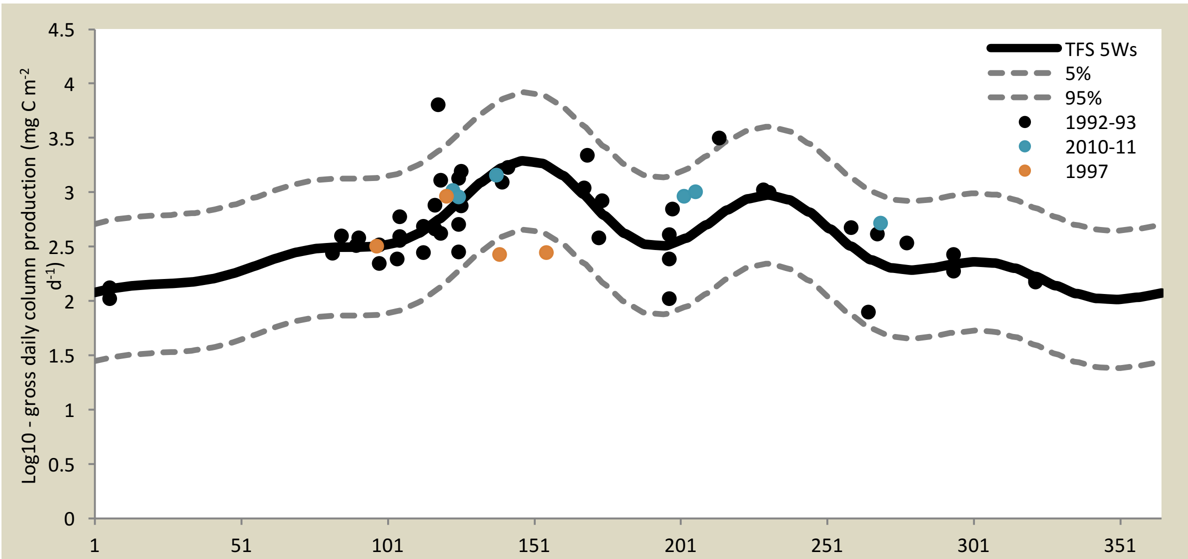

Figure 8: The annual cycle of primary production in the seasonal stratified offshore region (station 38A) of the western Irish Sea.

4.2 Fish and shellfish landings in the Irish Sea

The total annual catch (landings and discards where data for the latter are available) of fish and shellfish over the last 20 years (1992 - 2011) is shown in Fig. 9. The annual mean catch was 61,022 t y^{-1}. Landings are made up of a mixture of pelagic (resident and migratory) and demersal fish and a variety of shellfish (including crustaceans and bivalves). Changes in the fisheries have occurred over time due to change in total allowable catches (TACS), stocks and commercial viability. While the total annual catch has been relatively constant over the last 20 years, there has been a decline in the catch of demersal and pelagic fish which has been compensated for by an increase in the catch of shellfish. For the following assessment of the relationship between primary production and catch we have used a value of 14,522 t for the catch of demersal and pelagic fish. For the 2011 catch of *Nephrops* we have used a value of 12,845 t made up of 10,162 t landed and 2,683 t (21%) discarded. Bivalve catches were not included in any calculations.

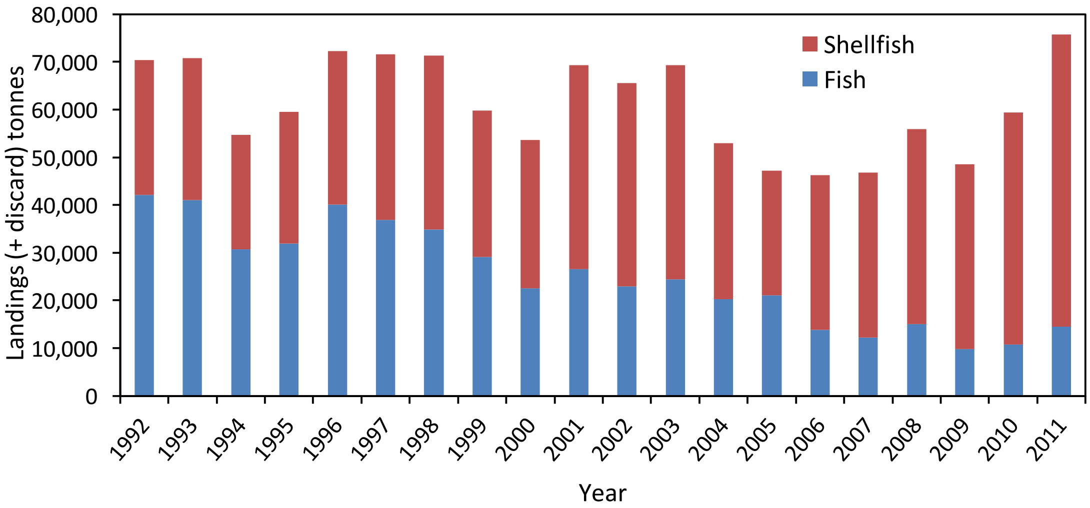

Figure 9: The annual landings of fish and shellfish from the Irish Sea between 1992 and 2011. (From ICES 2012)

5. Discussion

5.1 Long-term change in phytoplankton biomass and primary production

If as is generally accepted, nutrient availability (especially nitrogen) determines the level of production during the production season, then an increase in nutrients might be expected to result in an increase in primary production. Gowen et al. (2002) concluded that there was a low level of enrichment (~3 µM N [nitrate + nitrite]) in the western Irish Sea and a small increase in phytoplankton production is likely to have occurred. This argument is consistent with an increase in spring (May-June) chlorophyll (~2 mg m^{-3}) reported by Allen et al. (1998) at the Isle of Man time-series station approximately 5 km off the south west coast of the Isle of Man. For the production season as a whole however, Allen et al. (1998) found no change in phytoplankton biomass. A more recent comparison between data from the late 1960s (Isle of Man time-series) and data collected by DARD/AFBI between 1992 and 2004 also shows no major change in the level of phytoplankton biomass in the western Irish Sea (Gowen et al. 2008).

In contrast, Lynam et al. (2010) reported an increase (step change) in continuous plankton recorded (CPR) phytoplankton colour index (a proxy for chlorophyll) which occurred in 1989. Such a step change in biomass is unlikely to have resulted from a change in the nutrient status of the western Irish Sea (there has been no long-term change in nitrate concentration since the late 1970s, Gowen et al. 2008) but may have been related to the reduction in zooplankton reported by Lynam et al. (2010). Consistent with the time-series of nutrient data, the analysis presented here (Fig. 7 and 8) shows that there has been no change in phytoplankton biomass or production since 1991/92, (although this is after the 1980s step change reported by Lynam et al. 2010).

Our estimate of annual primary production (204 g C m^{-2} y^{-1}) for the western Irish Sea appears reasonable compared to estimates from the North Sea. Gieskes and Kraay (1975) gave an estimate of 250 g C m^{-2} for the central North Sea and estimates of 119 and 199 g C m^{-2} for the southern and central North Sea respectively were given by Joint and Pomroy (1993). Annual production for the Irish Sea as a whole is likely to be less than the 204 g C m^{-2} y^{-1} for the western Irish Sea but deriving a value is not straightforward because there are clear regional differences in the level of seasonal production (Gowen and Bloomfield 1996). For example, Gowen and Bloomfield (1996) estimated the average 1992 and 1993 seasonal production in the weakly stratified waters at the top of St. George's Channel as 101 g C m^{-2}. This is likely to be representative of the level of production in both St. George's Channel and the deep water to the south and east of the Isle of Man where the water column is vertically mixed for much of the year. In contrast, production in Irish coastal waters of the Irish Sea and in Liverpool Bay is higher. Gowen et al. (2000) gave a value of 182 g C m^{-2} y^{-2} for gross seasonal production in Liverpool Bay. Extrapolating the regional difference in production reported by Gowen and Bloomfield (1996) to the Irish Sea as a whole allows annual gross production to be approximated as 142 g C m^{-2}. We have used this figure when making comparisons between primary production and the yield of fish.

5.2 Primary production and fish yield

Plotting the 2011 Irish Sea catch against the value of 142 g C m^{-2} for annual Irish Sea gross production onto the Nixon (1988) and Iverson (1990) graphs (Fig. 4) suggests that the current (2011) Irish Sea catch is low relative to the level of primary production (Table 1). Using the 142 g C m^{-2} in Eq. 5 (Nixon 1988) gives a yield of 24.3 kg ha^{-1} wet weight of fish. Carrying out the same calculations but using Eq. 6 (Iverson 1990) gives a yield of 26.1 kg ha^{-1}. Both estimates are higher than the 2011 catch (3.2 kg ha^{-1}) and the 1992 catch of 42,044 t (= 8.7 kg ha^{-1}) but are similar to the catch data (17.1 kg ha^{-1}) given by Brander and Dickson (1984).

Brander and Dickson (1984) presented data on landings from the North Sea and Irish Sea for the period 1973 – 1978 (Table 2). For the Irish Sea, the mean, total international catch of demersal and pelagic fish was 17.1 kg ha^{-1}. Plotting this value with our estimate of annual primary production on the graphs in Fig. 4, shows that the mean 1973-1978 catch from the Irish Sea was broadly similar to the catch from other marine ecosystems. Similarly, the North Sea catch data from the same period are broadly consistent with both empirical relationships (assuming levels of annual primary production for the North Sea given above).

Table 1. Estimates of fisheries yields and landings from gross primary production for the Irish Sea and the North Sea using the Nixon (1988) and Iverson (1990) regression equations.

Equation	**Fisheries yield (kg ha^{-1})**		**Source**
Irish Sea	*Predicted*	*Landings*	
FP =1.55xlnPP-4.49	24.3	3.2	Nixon 1988
FC = -0.8+.024xACP	26.1	3.2	Iverson 1990
FP =1.55xlnPP-4.49	24.3	17.2[1]	Nixon 1988
FC = -0.8+.024xACP	26.1	17.2[1]	Iverson 1990
North Sea			
FP =1.55xlnPP-4.49			Nixon 1988
Northern	33.6	36.1	
Central	41.0	34.2	
Southern	18.5	15.6	
FC = -0.8+.024xACP			Iverson 1990
Northern	34.0	36.1	
Central	39.8	34.2	
Southern	20.6	15.6	

[1]catch data from 1973-1978 (From Brander and Dickson, 1978)

Table 2. Fish catch (kg ha^{-1}) from the North Sea and Irish Sea between 1973 and 1978. (Data from Brander and Dickson 1984)

	North Sea			**Irish Sea**
Fish group	*Northern*	*Central*	*Southern*	
Demersal	20.2	15.3	13.7	8.0
Pelagic	15.9	18.9	1.9	9.1
Shellfish	0.3	3.0	21.3	4.3
Area (x10^3 km^2)	253.6	270.4	64.5	48.2

In their comparison of fish landings in the Irish Sea and North Sea Brander and Dickson (1984) highlighted the lower catch in the Irish Sea relative to the North Sea and of several possible reasons arguing that the most likely was lower recruitment per unit area in the Irish

Sea. Brander and Dickson (1984) suggested that one possible cause of the lower recruitment was the short late production season (derived from CPR phytoplankton colour index data) in large parts of the Irish Sea: low phytoplankton production and a short-late production season characterized the Irish Sea and were consistent with the mismatch hypothesis of Cushing (1975). However, as noted above, when the 1970s catch data are plotted against the value of 142 g C m^{-2} for annual primary production on the graphs in Fig. 4, the catch from the Irish Sea was similar to other marine ecosystems including the North Sea. Furthermore, in the light of more recent data, it is evident that there is a complex interplay between the early life history stages of some fishes, the physical oceanography of the Irish Sea and the onset and timing of the production season (Dickey-Collas et al. 1996; Beggs et al. 2013). Nevertheless, it is evident that the Irish Sea fishery is considerably different to the fishery of the 1970s and it is important to bear in mind that the empirical relationship of Nixon (1988) is based on fisheries data from the 1970 and 1980s. It would be interesting to plot more recent data from the same sea areas studied by Nixon (1988) to see if the primary production to fisheries yield relationship has remained the same. A change in the slope of the regression line might indicate that there has been a change in ecosystem structure and functioning.

The catch of demersal and pelagic fish in the Irish Sea can be compared to primary production using the simple trophic-coupling equation of Ryther (1969) and by considering the amount of primary production required (PPR) to support the fisheries. The calculations (Table 3) show that the catch of demersal and pelagic fish represent between 2 and 5% of annual gross primary production assuming that the fish occupy a trophic level between 3.5 and 4. The estimates given in Table 3 above are based on gross production. However, not all of this is available to higher trophic levels. Phytoplankton utilises some (~49%) of the carbon fixed for respiration. Furthermore, some of the fixed carbon is recycled through the microbial loop and is not exported to higher trophic levels.

Table 3: Estimates of the primary production required (PPR) to support the Irish Sea fisheries based on equation 4 from Ryther (1969) and gross primary production (GPP) of 142 g C m^{-2} y^{-1} and with an assumed transfer efficiency of 16% between each trophic level.

Irish Sea PP: **6,844,400 t**onne C		Trophic level	PP available
	Ratio	1	6,844,400

PP (carbon) : Fish (wet wt)	471	2	0.16	1,095,104
PP (carbon) : Fish (carbon)	4713	3	0.0256	175,217
		3.5	0.01024	70,087
		4	0.004096	28,035

Trophic level	Primary production available (kg C ha^{-1} y^{-1})	Fish yield as % of PPR
T3	36.4	**0.8**
T3.5	14.5	**2.1**
T4	5.8	**5.2**

Iverson (1990) derived an empirical relationship between annual carbon production (ACP) and annual net nitrogen production (ANNP):

$$ANNP = -3.08 + 0.083 \times ACP \qquad (7)$$

Using eq. 7 and the estimate of 142 g C m^{-2} y^{-1} for gross production gives annual net nitrogen production of 8.7 g m^{-2}. Using a Redfield ratio of 6.6 (Redfield, 1958) to convert nitrogen to carbon and assuming algal respiration is 49% of the new carbon fixed, then 29.3 g C m^{-2} y^{-1} are available to higher trophic levels. Using this figure, the landings of demersal and pelagic fish at TL 3.5 and 4 represent between 10 and 25% of annual net new production. However, the 1992 catch of 42,044 t (at TL3.5) would require 29% of annual net new production and the 1970s catch of 17.1 kg ha^{-1} (82,422 t for the whole Irish Sea) would require 57% of annual net new production.

For fish at TL3.5, the trophic-dynamic model (eq. 4) of Ryther (1969) gives a fish production of 11.5 g wet weight m^{-2} y^{-1} (equivalent to 11.5 kg C ha^{-1} y^{-1}) based on an annual production of 142 g C m^{-2} y^{-1}. However, this is production not catch (yield). Iverson (1990) suggested that landings from marine waters with phytoplankton based food webs were on average 25% of fish production (Fig. 5). A production of 11.5 kg C ha^{-1} y^{-1} would therefore support a yield of 2.9 kg C ha^{-1} y^{-1}. The 2011 catch is only 0.3 kg C ha^{-1} y^{-1} which is ~10% of this potential yield.

5.3 Primary production and Nephrops norvegicus yield

According to Hill (2007) there is a simple and short food chain in the benthos of the western Irish Sea with *Nephrops* positioned at trophic level 3. The area of soft sediment in the western

Irish Sea is 3504 km^{-2} which represents 80% of the total Irish Sea *Nephrops* fishing ground (4380 km^{2}). The 2011 catch (landing + discard) was 12,845 t and assuming a wet weight to carbon conversion of 3.7% (Rowe, 1983) gives a yield of 475.3 t C y^{-1}. This is equivalent to 1.36 kg C ha^{-1} y^{-1} (or 0.14 g C m^{-2} y^{-1}). For *Nephrops* at TL3, approximately ~3% of the areal gross primary production in the western Irish Sea is required to support the yield of *Nephrops* in the western Irish Sea (Table 4).

The *Nephrops* landings in the Irish Sea can be compared to primary production using the simple trophic-coupling equation of Ryther (1969) (FP = ACP x E_1^n x c_1) and taking gross production of 204 g C m^{-2}; E_1^n to be 0.026 (TL3) and $c_1 = 27$ (based on the conversion of wet weight to carbon of 3.7%, Rowe, 1983). This gives a *Nephrops* production of 143.2 g wet weight m^{-2} y^{-1} (= 53 kg C ha^{-1} y^{-1}). The 2011 catch (yield) of 12,845 t of *Nephrops* (1.36 kg C ha^{-1} y^{-1}) represents 2.6% of the potential production.

Table 4: Estimates of primary production required (PPR) to support the *Nephrops* fisheries in the Irish Sea based on gross primary production.

Nephrops ground PP: 714,816 tonne C				
		Trophic level	E^n	PP available
	Ratio	1		714,816
PP (carbon) : *Nephrops* (wet wt)	55.7	2	0.16	114,371
PP (carbon) : *Nephrops* (carbon)	1504.0	3	0.064	45,748
			0.0256	18,299

Trophic Level	Primary production available (kg C ha^{-1} y^{-1})	*Nephrops* yield as % of PPR
T2	326.4	***0.4***
T2.5	130.6	***1.0***
T3	52.2	***2.6***

An alternative approach to looking at the relationship between primary production and the yield of *Nephrops* is to construct a simple carbon budget (Fig. 3). The first step is to estimate net new production from gross production. As discussed above not all of the gross production is available to higher trophic levels. Assuming annual gross production to be 204 g C m^{-2}, eq. 7 (Iverson 1990) gives annual new nitrogen production of 13.9 g m^{-2}. Using a Redfield ratio of 6.6 (Redfield, 1958) to convert nitrogen to carbon then annual new carbon production = 91.4 g C m^{-2}. Assuming algal respiration is 49% of gross production, then 46.6 g C m^{-2} y^{-1} of new net production is available to higher trophic levels.

The second step is to estimate how much of the new net production is available to the benthos. In the absence of direct measurements of sedimentation rates, simple empirical relationships can be used to estimate the amount of phytoplankton carbon that settles to the seabed. Suess and Müller (1980) gave the relationship:

$$\text{Flux } C_{org} = 5.9 \text{ x depth}^{-0.616} \text{ x productivity} \qquad (8)$$

Trimmer et al. (1999) found that this relationship gave a reasonable estimate of the input of phytoplankton carbon to the benthos during the 1997 spring bloom when compared to the input based on measurements of sediment oxygen demand. Assuming water depth to be 90 m, then the net input of new production to the benthos would be 17.2 g C m^{-2} y^{-1} (or 17.2kg C ha^{-1} y^{-1}). The amount of carbon available for animals at TL3 would be 4.4 kg C ha^{-1} y^{-1}. The *Nephrops* catch (1.4 kg C ha^{-1} y^{-1}) represents 31% of the available phytoplankton carbon.

In this section we have attempted to compare estimates of primary production with the catch of demersal and pelagic fish and with the catch of *Nephrops.* Deriving estimates of primary production for the Irish Sea as a whole and calculating the primary production available for different trophic levels is not a trivial task and involves assigning values to particular variables such as trophic transfer efficiency. Similarly, estimating the catch (landings and discards) for the Irish Sea is not straightforward. There are errors in reporting, some discarding is not quantified and the landings include several migratory species which only spend a small proportion of their time feeding in the Irish Sea. Nevertheless, our analysis shows that if the level of primary production in the 1970s was similar to the current level, then the 1970s Irish Sea catch of demersal and pelagic fish was similar to other marine ecosystems. However, it is clear that over the last 20 years, the catch (landings + discard) of demersal and pelagic fish has declined (Fig. 9) as stocks have declined and the catch is now much lower than might be expected from the empirical relationship of Nixon (1988) and the simple trophic-dynamic model of Ryther (1969).

The catch in the Irish Sea is much reduced and the biomass of top predator fish such as cod and whiting is now much lower. Whether these changes have been driven by overfishing (top down) or ecological change (bottom up) pressure or a combination of both is a much debated topic and not just in relation to the Irish Sea.

Has primary production increased while fish catch has declined? This seems unlikely, at least over the last 20 years, although Lynam et al. (2010) reported a step change increase in CPR phytoplankton colour index in the Irish Sea in the late 1980s. For fisheries in Pacific coastal waters of North America, Ware and Thompson (2005) concluded that 87% of the spatial variation in long-term, mean resident fish production was controlled by bottom-up trophic interactions and that in addition to fishing pressure; bottom-up control (decline in zooplankton abundance resulting from an ecosystem regime shift) contributed to a decline in fish yields. Lynam et al. (2010) also reported a decrease in planktonic copepods (and an increase in gelatinous zooplankton). The extent to which these changes may have propagated up through the food chain and influenced higher tropic layer production (including the fisheries yield) requires further study.

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