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Influence of planktonic foodweb structure on a system's capacity to support pelagic production: an inverse analysis approach

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Abstract:

Coupled plankton/small pelagic (SP) fish systems were analysed to assess how foodweb structure influences the export of carbon to pelagic fish during the spring bloom in the Bay of Biscay. The investigation of carbon export flows through inverse analysis was supplemented by estimating the carrying capacity for pelagic fish production by applying linear programming. A planktonic foodweb dominated by microbial pathways had the highest trophic efficiency owing to the tight coupling between planktonic trophic levels and predation pressure on mesozooplankton by fish. Moreover, the magnitude of the gap between carrying capacity and estimated carbon export was related to the size structure of primary producers, with the picophytoplankton-based foodweb having the smallest gap and the microphytoplankton-based one the largest gap. Planktonic foodwebs dominated by small autotrophic cells channelled most of their available carbon to pelagic fish production, whereas foodwebs dominated by large phytoplankton were better suited to benthic communities with a large loss of carbon through sedimentation. Although the total carbon available to higher trophic levels does not vary with the size of the main primary producers, the potential export to SP fish depends on the structure of the planktonic foodweb.

Keywords: Bay of Biscay ; carbon export ; carrying capacity ; inverse analysis ; planktonic foodweb ; small pelagic fish

INTRODUCTION

The fate of primary production and the flux of biogenic carbon in the oceans are major concerns in biological oceanography (e.g. Duarte and Cebrian, 1996). The fate of primary production depends on the path carbon takes within the planktonic food web. Two simplified patterns, the grazing food chain and the microbial food web, have been distinguished based on the size of the main algal producers (Azam *et al.*, 1983, Sommaruga, 1995). The most common view indicates that the planktonic food web exports biogenic carbon mostly during diatom blooms (e.g. Cushing, 1989, Legendre, 1990) when the algal cells are either directly grazed by metazoans or sink out of the photic zone (Legendre, 1990). This situation (upwelling, coastal waters) corresponds to the most productive world wide fisheries (Cushing, 1989). The opposite situation is found in oligotrophic waters where the main primary producers are pico-nanophytoplankton that are not directly grazed by mesozooplankton (Capriulo *et al.*, 1991). Within this kind of ecosystem, the biogenic carbon is recycled through the microbial food web before it reaches metazoans (Cushing, 1989, Legendre and Le Fevre, 1995). This type of planktonic food web structure corresponds to the lowest export rates of biogenic carbon (Legendre and Rassoulzadegan, 1996) and to less productive fisheries. Regarding the two planktonic food web functioning described above, the food web structure has an influence on the system's capacity to support benthic and/or pelagic fish production (Sommer *et al.*, 2002). Thus, describing the planktonic food web structure and functioning is essential to understand the trophic links between plankton communities and higher trophic levels.

In the Bay of Biscay, small pelagic fish such as anchovy or sardines are an important economic resource. In spring, these fish are mainly localized on the continental shelf which corresponds to the peak spawning period (between May and July) (Motos *et*

al., 1996). Previous studies have shown the occurrence of winter diatom blooms on the continental shelf of the Bay of Biscay (e.g. Gohin *et al.*, 2003) that lead to the onset of phosphorus limitation in early spring (e.g. Herbland *et al.*, 1998). As a consequence, spring corresponds to a transient situation from a system dominated by large-sized phytoplankton (winter diatom bloom) to one dominated by small-sized phytoplankton that are better competitors in phosphorus-limited conditions (Herbland *et al.*, 1998). During spring, the planktonic food web in the Bay of Biscay is then based on multivorous trophic flows (Legendre and Rassoulzadegan, 1995). The consequences of this specific planktonic food web dynamics on carbon export through sedimentation have been studied using inverse analysis (Marquis *et al.*, 2007). In that study, phytoplankton size was not a determining factor in downward export (E, i.e. sedimentation) (Legendre and Rivkin, 2002) and bacterial activity had potentially a higher control on relative carbon export than phytoplankton size structure. In the present study, we focused on examining the export to the higher pelagic food web (F) (Legendre and Rivkin, 2002). We focused specifically on small pelagic fish production that is an important economic resource in this area. Inverse analysis method (Vézina and Platt, 1988, Vézina, 1989) was used to reconstruct the entire food web combining plankton and fish compartments and to estimate carbon flows.

The overall goal of this study was to specify the relationship between planktonic food web functioning and the system capacity to export biogenic carbon to small pelagic fish (F) during spring. We investigated two different estimates of export to higher pelagic levels: one is an export consistent with the available data on fish abundance and the second is a potential export, i.e. the maximum carbon flux that can support pelagic fish production given constraints on primary production and food web structure (Fmax). Our question was whether there is a substantial gap between the two estimates and whether food web structure influences the difference between real export and capacity of export. This is the

first time inverse analysis has been used to investigate the productive capacity of fisheries ecosystems.

MATERIAL AND METHODS

Study site

The Bay of Biscay (Fig. 1) is an open bay within the eastern Atlantic Ocean. This bay is characterized by a large continental shelf (up to 200 km wide). Data for the study were obtained from the PEL2001 oceanographic cruise (Fig. 1) in spring 2001. Plankton was sampled at three stations (A, 47°11N-3°15W, 70-m deep; B, 47°04-4°19W, 129-m deep; and C, 46°55N-05°17W, 381-m deep; respectively 11,12 and 13 May 2001) located on a Loire plume transect across the continental shelf (A being the station closest to the Loire estuary and C the farthest) (Fig. 1). Based on the available data at the three stations, three food webs have been constructed using inverse analysis.

Plankton and fish data

Data about plankton ecosystem, i.e. productions and biomass (Table 1), were sourced from Marquis *et al.* (2007). With regard to the variation in field data estimation over one-week survey (Biomet cruises, cf. Marquis *et al.* 2007), the overall estimate error for plankton input data was assumed to be less than 20%. Before comparing the three systems, the impact of this uncertainty in the input data on the carbon flow estimates has been tested with a sensitivity analysis where each input data was individually changed by plus and minus 20% (cf. Marquis *et al.* 2007).

The small pelagic fish species studied were: anchovy (*Engraulis encrasicolus*), Atlantic horse mackerel (*Trachurus trachurus*), Atlantic and chub mackerel (*Scomber*

scombrus and *S. japonicus*), sardine (*Sardina pilchardus*) and sprat (*Sprattus sprattus*). Fish species were regrouped into functional compartments based on published feeding requirements (derived from Mehl and Westgard, 1983, Tudela and Palomera, 1997, Plounevez and Champalbert, 2000, Bode *et al.*, 2003, Sanchez and Olaso, 2004):

- Small Pelagic 1 (SP1): strict zoophagous (anchovy, sprat, small horse mackerel ≤ 16 cm, small sardine ≤ 18 cm and small Atlantic + chub mackerel ≤ 24 cm).
- Small Pelagic 2 (SP2): phyto-zoophagous (large sardine > 18 cm).
- Small Pelagic 3 (SP3): meso and macrozoophagous and ichthyophagous (large horse mackerel > 16 cm and large Atlantic + chub mackerel > 24 cm).

Small pelagic fish biomasses (Table 1) were estimated from acoustic surveys run during daytime at 10 knots along cross-shore transects from the coast (20 m isobath) to the edge of the continental shelf (250 m isobath). Transects were parallel to each other and set at approximately 12 nautical miles from each other. Trawl hauls run in conjunction with the acoustic surveys allowed us to assess the proportion of each species of small pelagic fish within each transect (Petitgas *et al.*, 2003). The biomass of species was then determined according to its average size and wet weight collected during trawls. The estimate error of this method is assumed to be around 12.5% (Petitgas, 1993). The conversions from wet weight (WW) to dry weight (DW) and carbon biomass (CB) were done by applying the ratios: DW = 0.30 WW and CB = 0.45 DW (Karakoltsidis *et al.*, 1995). We took fish movements into account during 24 h by calculating the mean biomass of small pelagic fish within a radius of 15 nautical miles around each station (A, B and C).

Methods to construct and analyze food webs

Inverse analysis is a numerical method for developing complete, steady state food web models (Vézina and Platt 1988, Vézina 1989). The *a priori* linear model (Fig. 2) links

observations to unknown flows that need to be estimated. Inverse analysis uses field estimates and other data sources to develop a network of equations and inequalities in order to build the best estimates of food web flows. The solution selected is the minimum of a norm ('parsimony principle'). A complete description of the method is in Marquis *et al.* (2007). The algorithm of resolution from Vézina and Platt (1988) was programmed by G. A. Jackson using the software Matlab©.

In the present work, the method used in Marquis *et al.* (2007) was subjected to two modifications concerning (1) the coupling of the small pelagic fish compartments with the plankton ecosystems and (2) the estimation of the carrying capacity.

Coupling the fish compartments to the planktonic systems

We used concurrent fish abundance data to constrain the flow from plankton to higher consumers. This is something that is rarely done, if ever, in inverse analysis where the focus is usually on passive carbon export and export to fish is either ignored or treated as a free parameter.

The simple *a priori* model (Marquis *et al.*, 2007) was adapted to include three small pelagic fish compartments (Fig. 2). The new *a priori* model included 50 average flows of carbon below one square meter of the photic zone during one day (Table 2).

The 22 inequalities concerning fish compartments described their consumption (Q) and production (P). Those inequalities were calculated with the mean ratios of consumption on biomass (Q/B) and production on biomass (P/B) of each small pelagic fish group (Table 3). The highest and the lowest values of those ratios found in the literature for each species were used to build the interval limits for each trophic group (derived from Hoenig, 1983, Palomares and Pauly, 1989, Pauly, 1989, Ainsworth *et al.*, 2001, Harvey *et al.*, 2003, Trites, 2003, Sanchez and Olaso, 2004). The aggregate Q/B and P/B ratios for

each fish compartment were the sum of the ratios for each species making up the compartment, weighted by the relative biomass of each species. The egestion (feces production) flux ranged between 10 and 20% of the consumption (derived from Klumb, 2002). The diet of SP2 and SP3 fishes was assumed to comprise between 40 and 60% mesozooplankton while SP1 were assumed to consume 100% mesozooplankton (derived from Mehl and Westgard, 1983, Tudela and Palomera, 1997, Plounevez and Champalbert, 2000, Klumb, 2002, Bode *et al.*, 2003, Sanchez and Olaso, 2004). Finally, predation of SP3 fishes on organisms not included in the model was assumed to vary between 5 and 15% of the sum of the total plankton losses (other predation on mesozooplankton and sedimentation of microphytoplankton and detritus) that correspond to the euphausiid diet (derived from the euphausiid ingestion estimated in Sanchez and Olaso, 2004).

Estimation of the carrying capacity

We used linear inverse modeling to calculate F, the least-squares estimate of the export that supports fish production during spring in the Bay of Biscay. We also used linear programming (LP) (Luenberger, 1984) to calculate Fmax, the potential carbon export. The goal of this carrying capacity analysis was to obtain the theoretical maximum production of small pelagic fish supported by each of the three planktonic food webs. In order to simplify the analysis, only one fish compartment production was directly maximized, while the other two increased in relation to its maximization. The ratios between production and consumption of each fish compartment were also preserved in the estimation of the carrying capacity. The results of the inverse analysis calculations were used in order to fix the P/Q ratio of each SP compartment and the ratios of SP1 and SP2 productions to SP3 production. Then, the linear programming was applied to maximize

SP3 production. LP produces the highest value of SP production (Fmax) that is supported by the system (without changing any input data and constraints).

Network analysis

The 'Netwrk 4.2' program (Ulanowicz, 1999) was used to calculate indices describing the modeled food web. In this study, the network indices used were the effective trophic level of each compartment and the Finn cycling index (FCI, Finn, 1976). The effective trophic level of a compartment corresponds to its trophic position when the food web is simplified into a simple linear food chain. FCI is defined as the ratio of the sum of carbon flows in cyclic pathways to the sum of all carbon flows in the food web.

RESULTS

Food web functioning

Plankton

Total net production of the three size classes of phytoplankton (Fig. 3) was high at the three stations, but the total net primary production was 1.4 times higher at station A (1180 mgC m^{-2} d^{-1}) than at the other stations. The proportion of production by small phytoplankton (Ph1 and Ph2) was high in B and C (98 and 80% of total net primary production, respectively) and relatively lower in A (48% of the total net primary production).

Net bacterial production was low at the three stations and represented less than 8% of the total net primary production (Table 4). The net protozoan production as a proportion of total net production was similar in A and C but two times higher in B (Table 4). The mesozooplankton production represented similar proportions of the total primary

production (PP) in the three food webs (Table 4). As a consequence of the stronger role of protozoa within the diet of mesozooplankton, the mesozooplankton effective trophic level was the highest in the mid-shelf station (2.65, Table 4).

The FCI (Table 4) indicated that food webs in stations A and C had more significant cycling pathways than in station B, i.e. the amount of carbon flowing through the DOC and the detritus compartments were higher in A and C than in B (Table 4).

Pelagic fish

The total net production of pelagic fish was highest in station B (in relation to the high biomass of SP3 measured around the station, cf. Table 1) with more than 20 mgC m^{-2} d^{-1} (Fig. 4a). The total net production of pelagic fish was similar in stations A and C at 11.3 and 12.2 mgC m^{-2} d^{-1}, respectively (Fig. 4a). Although the compartments SP1 and SP3 were the main components of the fish biomass in A (Table 1), most of the fish production was due to SP1 only (Fig. 4a). In station C, the proportions of the three fish compartments were roughly equal in total biomass and production (Table 1 and Fig. 4a).

The predation on mesozooplankton by small pelagic fish was highest in B with a mesozooplankton consumption of 6, 10 and 96 mgC m^{-2} d^{-1} by SP1, SP2 and SP3, respectively (Table 2). Predation on mesozooplankton by small pelagic fish was slightly lower in A and in C with total consumptions of 56 and 84 mgC m^{-2} d^{-1} (Table 2). The predation of small pelagic fish on mesozooplankton was not the major carbon outflow in A (31% of the total carbon outflows from mesozooplankton, Fig. 4b); other predators such as euphausiids or other fish consumed 69% of the available biomass of mesozooplankton in A and less than 32% in B and C of carbon available from mesozooplankton prey (Fig. 4b).

Export to pelagics and carrying capacity

In terms of export (F), station B showed the highest ratio of total net small pelagic (SP) production to total net Primary Production (2.4%, Fig. 5), while station A showed the lowest value (1.0%, Fig. 5). The difference between the export (F) and the capacity (Fmax) was highest in station A (1.0 to 9.0%, Fig. 5). The two values (F and Fmax) were very similar in station B (2.4 and 2.5%, Fig. 5) and the capacity in station C was almost 3 times higher than the export (1.4 to 3.8%, Fig. 5). In all three systems, as a consequence of constraining predation fluxes at their maximum limits, linear programming led to a considerable decrease (virtually reach 0) in microphytoplankton sedimentation and other predation on mesozooplankton whereas the sedimentation of detritus increased as a consequence of higher mesozooplankton ingestion (detritus mainly composed of fecal pellets).

DISCUSSION

Planktonic food web functioning

Net primary production was high at the three stations (> 800 mg C m^{-2} d^{-1}) and corresponded to typical values found during spring bloom in temperate waters such as the Baltic Sea (> 1000 mgC m^{-2} d^{-1}; Tremblay *et al.*, 2002) or the Gironde plume in the Bay of Biscay (Laborde *et al.*, 1999). Moreover, bacterial to primary production ratios were very low, as also observed during spring in upwelling coastal area off the northern Spanish coast (0.04; Teira *et al.*, 2003). The three food webs represented different stages of the spring bloom on the continental shelf of the Bay of Biscay (Marquis *et al.*, 2007). Coastal spring blooms generally occur first near the coast or river mouths (stratification due to low salinity, combined with relatively high nutrient levels) before progressing offshore (e.g. Yin *et al.*, 1996). However, in our study, the microphytoplankton bloom seems less advanced inshore than mid-shelf (station B is located 60 nautical miles further offshore

than station A). This observation is consistent with satellite observations (Gohin *et al.*, 2003) where the spring bloom appeared in the middle of the continental shelf before the coastal area. This situation may be due to the high turbidity of the river plume waters. The resulting low light environment due to river discharge may have delayed the inshore bloom (e.g. Iriarte and Purdie, 2004).

As shown in Marquis *et al.* (2007), sensitivity analysis, done by changing the input data by plus or minus 20%, revealed that the inverse solutions clearly separated the three models based on their different flow structure. Thus, combining the observations on the bloom timing with those on microbial flows in each food web resulted in the description of three distinct functioning; the inshore station was dominated by direct trophic pathways (i.e. microphytoplankton to metazoans); the offshore station was in transition from a winter situation with high carbon cycling, to a spring situation with high microphytoplankton production; the mid-shelf station represented an intermediate situation between a food web dominated by direct pathways to one dominated by microbial pathways (Legendre and Rassoulzadegan, 1995, Marquis *et al.*, 2007).

Predation on mesozooplankton

The differences in fish production observed among the three stations were related to fish biomass. Since the three fish compartments showed similar ranges of P/B and Q/B ratios (Table 3), the spatial distributions of each fish species have an effect on the total pelagic fish production calculated at each station. During spring 2001, large sardines (SP2) were distributed along the shelf break such as in spring 2000 (Petitgas *et al.*, 2006), the smallest pelagic fish such as sprat and anchovy (SP1) were located close to the coast and the larger fish such as chub mackerels (SP3) were mainly distributed in mid-shelf.

Therefore, the highest production observed in mid-shelf is related to the very large biomass of SP3 (> 10 gC m^{-2}) due to high mackerel abundances.

However, the method used to obtain fish biomass data (i.e. combining acoustic surveys and trawl observations) may induce an estimate error (Petitgas *et al.*, 2003). In order to assess whether there was a relationship between fish biomass estimation errors and our carbon flow calculations, we tested the three fish biomasses individually at each station (results not shown). We did not explore effects of combined errors between them. We changed the selected biomass by plus or minus 10% (error margin considered for the fish biomass estimation) and reran the inverse analysis. The resulting carbon flows within the planktonic food web did not differ from the original values by more than 10%. Thus, the uncertainty of the fish biomass data will have had little effect on the final differences between F and Fmax resulting from our analysis, when comparing each food web.

The spring conditions of the three food webs may have allowed a large export of carbon to planktivorous fish, since primary production reached high levels and planktonic grazers (protozoa and mesozooplankton) were present in the three food webs (Legendre and Rassoulzadegan, 1996, Marquis *et al.*, 2007). The flow of carbon available to planktivores was sufficient in the three food webs to cover the food requirements of small pelagic fish present in the environment. In fact, small pelagic fish did not appear to be the most important predator of mesozooplankton inshore (30% of total predation on mesozooplankton) and represented between 60 and 65% of the total predation on mesozooplankton in mid-shelf and shelf edge stations, respectively. This relatively low level of predation on mesozooplankton suggests that a large fraction of the mesozooplankton production may be available for other planktivorous organisms, such as suprabenthic zooplankton (euphausiids and mysiids) or macrozooplankton (medusa or large tunicates). The observations made on the biomass and the diet of such

macrozooplankton in the area close to the Bay of Biscay may confirm this inverse analysis result. For example, macrozooplankton biomasses are high during springtime in areas close to the Bay of Biscay, such as St Brieuc Bay (Vallet and Dauvin, 1999) and these biomasses are dominated by mysids. In the Baltic Sea, the diet of mysids is composed of a large proportion of copepods and rotifers throughout the year (Rudstam *et al.*, 1992) and euphausiids of the North-East Atlantic Ocean are important copepod predators (Bamstedt and Karlson, 1998). Moreover, along the Cantabrian coast, mysids and euphausiids consume approximately 60% of the total carbon available from mesozooplankton over one year (Sanchez and Olaso, 2004). Despite the importance of the mysid and euphausiid populations (as well as other possible planktivorous fish) in the pelagic food web of the Bay of Biscay as revealed by our model, the distribution and biomass of those predators have never been as intensively studied as the small pelagic fish. With regard to our model results, we argue that there is an urgent need in the study of mysid and euphausiid distribution, biomass and predation impact within the Bay of Biscay.

Trophic efficiency from primary production to pelagic fish

The export to pelagic fish (F) corresponded to the relative fish production (ratio of net pelagic fish production to net primary production) and varied between 1 and 2.4 % in the three food webs. The value of 2.4 % found at the mid-shelf station seemed high compared to what is currently assumed in the literature. The general view of pelagic ecosystems assumes an ecological efficiency of 10 % between each trophic level (Pauly and Christensen, 1995). Therefore, if planktivorous fish occupy the third trophic level in the food web, as generally assumed, this means that fish production would not exceed 1% of the primary production. Indeed, the small pelagic fish trophic level may change with the planktonic food web structure and the resulting relative fish production may be higher than

1% of the primary production (in upwelling areas, Ryther, 1969) as well as far lower (Iverson, 1990). In our study, the high relative fish production found at mid-shelf mean that the trophic efficiency between each trophic level in the food web was higher than 10% (e.g. Sommer *et al.*, 2002). Such a high trophic efficiency might have been due to tight coupling between trophic levels (Gaedke and Straile, 1994). Gaedke and Straile (1994) explained that this situation would happen if the primary production was nutrient limited and the microbial pathways were dominating the carbon pathways in the planktonic food web. Such situations can be observed at site B where the recent microphytoplankton bloom led to a nutrient limitation and the production of picophytoplankonic cells supported active protozoan grazing (high relative protozoa production, Table 4). This hypothesis is reinforced by the very low Finn Cycling Index measured at the mid-shelf station (Table 4) that shows very little recycling activity despite the importance of microbial communities (protozoa). Moreover, we argue that the predation control on mesozooplankton by the very large population of planktivorous fish at this site (SP3) may have enhanced the tight coupling at lower trophic levels and so the final trophic efficiency of the planktonic food web.

Support of benthic and pelagic production

As shown in Marquis *et al.* (2007), the relative amount of carbon exported from mesozooplankton (i.e. carbon available for predation on mesozooplankton) does not vary with the size of the dominant primary producers: 14.32 to 15.81% at all stations (ratios of net mesozooplankton production to net primary production, Table 4). Moreover, the differences observed between the values of relative export to pelagic fish (F) at each station are also rather low (1 to 2.4%).

On the other hand, the gap between export to pelagic fish (F) and carrying capacity (Fmax) was very different between the 3 stations, with the highest difference observed at the inshore station and the lowest at the mid-shelf station. These dissimilarities may be related to their distinctive food web structure (Fig. 6). The *in situ* conditions of the inshore station led to the export of large amounts of carbon, mainly through sedimentation of fresh microphytoplankton cells and detritus. When maximizing pelagic fish predation, those carbon flows were reduced and the corresponding amount of carbon was transferred towards the fish, resulting in a very high carrying capacity. Legendre (1990) and Cushing (1989) both concluded that microphytoplankton blooms allow the highest export of carbon. They also said that areas with microphytoplankton bloom sustain the largest fisheries but the relatively low export to pelagic fish of the inshore food web indicated that the microphytoplankton-based food web was not an optimal situation for strict pelagic fish production. We therefore argue that the inshore food web seemed configured to support demersal and benthic productions (Fig. 6) through downward export of detritus and microphytoplankton aggregates (Richardson *et al.*, 2000). However, due to the relatively shallow depth of the inshore station, pelagic fish should be able to consume descending particles. This possibility is not included in the present model but should be taken into account in future studies in order to confirm the proportion of the spring bloom production actually reaching the benthos in the inshore food web.

At mid-shelf, primary production was almost exclusively exported to the pelagic fish production and the general trophic efficiency was high. The capacity (Fmax) of the mid-shelf station was equivalent to the export (F), meaning that the maximum level of pelagic fish production supported was reached under the *in situ* conditions. Despite low observed biomass, the protozoa community was very active in this food web in response to the importance of the picophytoplanktonic production (Legendre and Rassoulzadegan, 1996).

Such as in the example of Northeast Water Polynya (Pesant *et al.*, 2000), the downward export of carbon was low in this planktonic food web dominated by small phytoplankton. Downward carbon fluxes may still exist through the sedimentation of the copepod faecal pellets; however, those pellets may not sink as fast as diatom aggregates and therefore may not be a direct energy source for benthic metazoans (Legendre and Rivkin, 2002). As a consequence of those low sedimentation flows, the picophytoplankton-based food web showed the highest export (F) of carbon to pelagic fish but the lowest carrying capacity (Fmax) (Fig. 6). Thus, the picophytoplankton-based food web with high protozoa activity emerged as the optimal situation to support pelagic production. At last, the shelf edge food web that included both microbial and herbivorous pathways was an intermediate situation between the two extremes (inshore and mid-shelf) with an intermediate carrying capacity (Fmax) and an intermediate gap between F and Fmax (Fig. 6). Both pelagic and benthic productions were then supported in the *in situ* conditions of that multivorous food web.

CONCLUSION

These three situations illustrated the complexity of the existing relationships between planktonic food web and carbon export in the ocean (Legendre and Rassoulzadegan, 1996). With equivalent levels of primary production, the three food webs differed from one another through the number of steps existing between the primary production and planktivorous fish and through its capacity to support pelagic production as well as benthic production. In Marquis *et al.* (2007), the analysis of simple plankton food webs led to the conclusion that the total amount of carbon available to pelagic predators was less controlled by the size structure of the primary producers than by the bacterial to primary production ratio. In the present study, although this conclusion is confirmed, it is shown that the main primary producer size and food web functioning were directly influencing the

carrying capacity of the planktonic food web and its relative support to pelagic and/or benthic fish production. In general, studies considering the relationship between plankton and fisheries take into account neither the size structure of the primary producers nor the planktonic food web functioning (e.g. Iverson, 1990). Considering the results of the present study, we argue that distinction between amounts of carbon available, carbon flows to pelagic fish and carrying capacity of the ecosystem needs to be carefully taken into account and therefore plankton food web functioning should not be neglected anymore in fisheries studies.

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Figure captions

Figure 1: Map of the Bay of Biscay showing the three stations of the study. PEL-A for station A, PEL-B for station B and PEL-C for station C. Dashed line is a schematic representation of the continental shelf limits.

Figure 2: *a priori* model used to build the coupled small pelagic fish/plankton systems. Definitions of abbreviations are Ph1: picophytoplankton (<2µm), Ph2: nanophytoplankton (2-20µm), Ph3: microphytoplankton (>20µm), Bac: bacteria, Pro: protozoa (ciliates and flagellates, 20-200µm), Mes: mesozooplankton (>200µm), SP1: small pelagic fish 1, SP2: small pelagic fish 2, SP3: small pelagic fish 3, Det: detritus and DOC: dissolved organic matter.

Figure 3: Contribution of the 3 phytoplankton size-classes to the net total primary production (mgC m^{-2} d^{-1}) for the three food web systems. Ph1: picophytoplancton, Ph2: nanophytoplankton and Ph3: microphytoplankton.

Figure 4: a) Contribution of each compartment of small pelagic fish to the total fish production in mgC m^{-2} d^{-1} and **b)** Fate of the carbon outflows from mesozooplankton in % of the total predation on mes: 177.7, 136.8 and 123.2 mgC m^{-2} d^{-1}, respectively at sites A, B and C. SP1: small pelagic fish 1 (strict zoophagous: anchovies, sprats, small horse mackerels < 16 cm and small sardines < 18 cm), SP2: small pelagic fish 2 (phyto-zoophagous: large sardines > 18 cm), SP3: small pelagic fish 3 (meso-macrozoophagous and ichtyophagous: large horse mackerels > 16 cm and atlantic + chub mackerels), Other: others predators of mesozooplankton (euphausiids, larger fish, etc.).

Figure 5: Ratios of the total small pelagic fish production on total net primary production (%): export (F) and capacity (Fmax) for the three food web systems.

Figure 6: Schematic synthesis of the results with emphasis on carbon export toward fish populations.

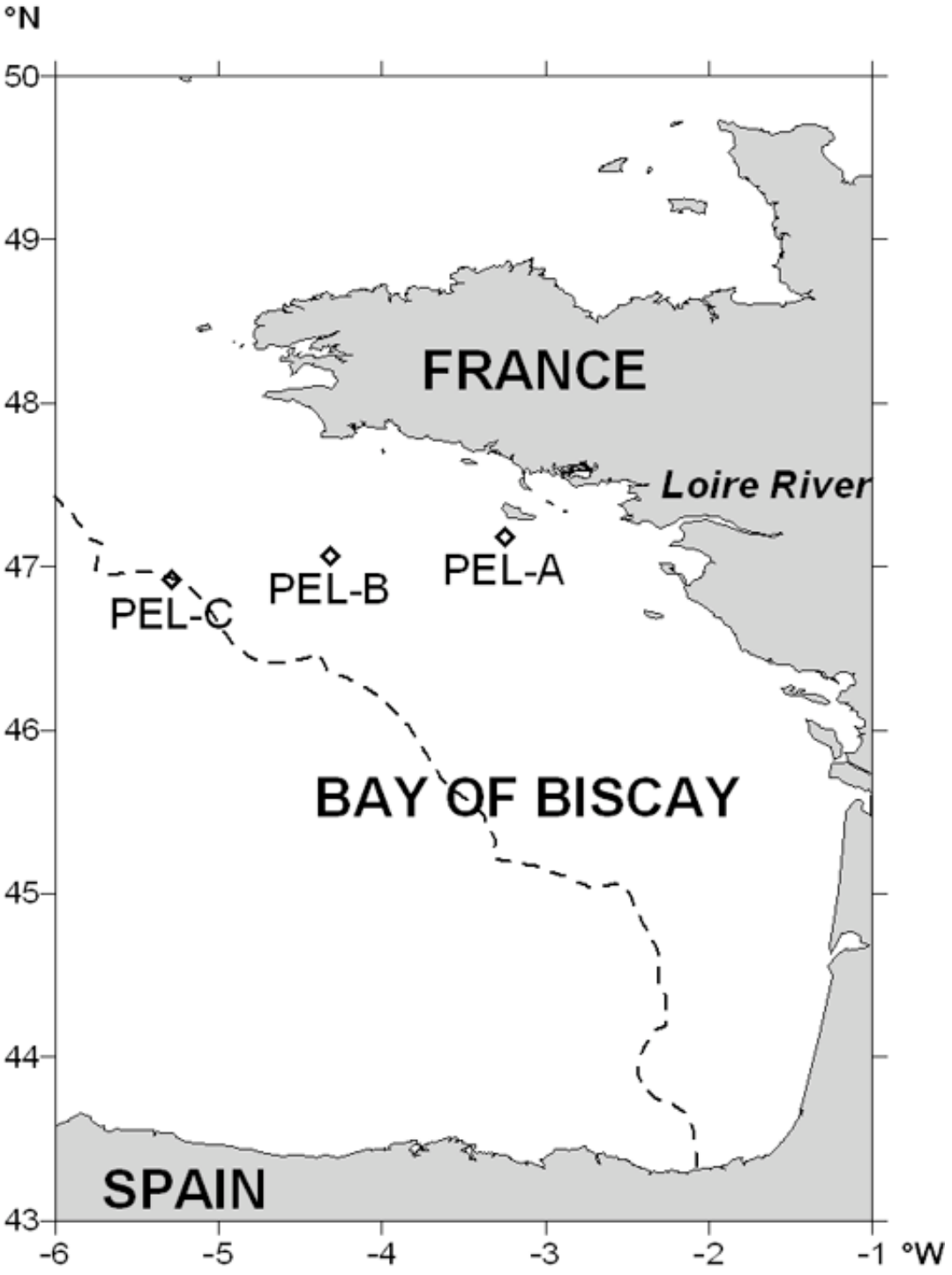
°N
50
49
48
47
46
45
44
43
-6
-5
-4
-3
-2
-1 °W
FRANCE
Loire River
PEL-A
PEL-B
PEL-C
BAY OF BISCAY
SPAIN

Fig. 1

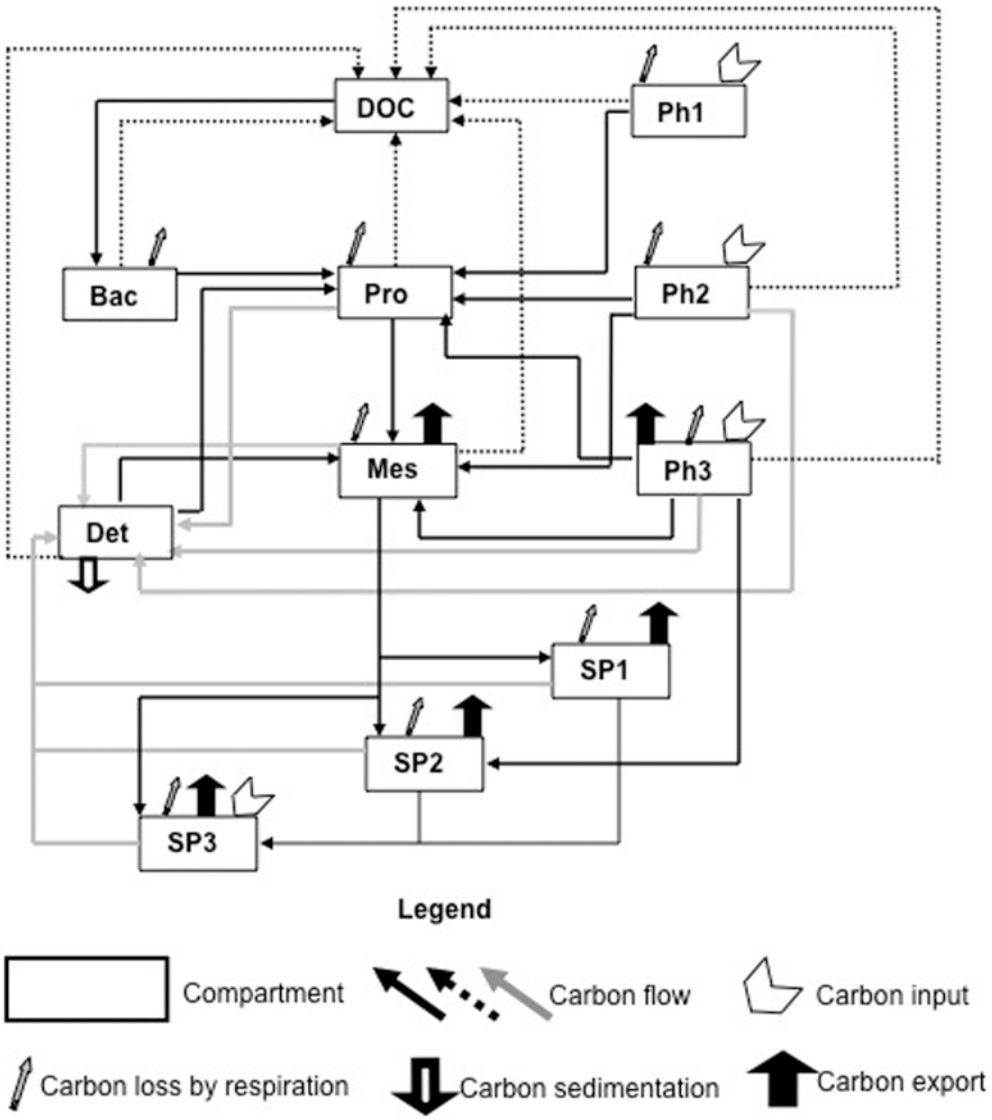
DOC
Ph1
Bac
Pro
Ph2
Mes
Ph3
Det
SP1
SP2
SP3
Legend
Compartment
Carbon flow
Carbon input
Carbon loss by respiration
Carbon sedimentation
Carbon export

Fig. 2

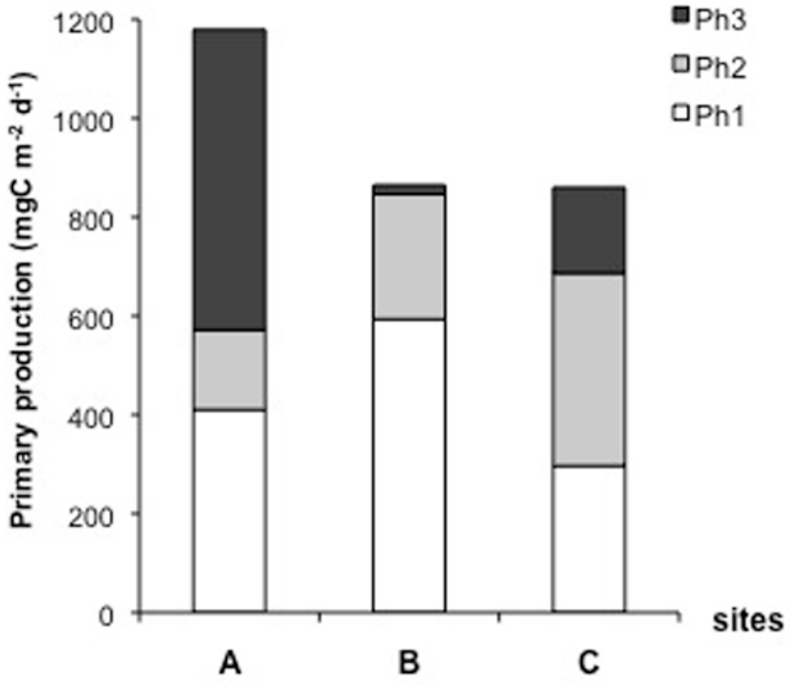
Ph3
Ph2
Ph1
Primary production (mgC m-2 d-1)
1200
1000
800
600
400
200
0
A
B
C
sites

Fig. 3

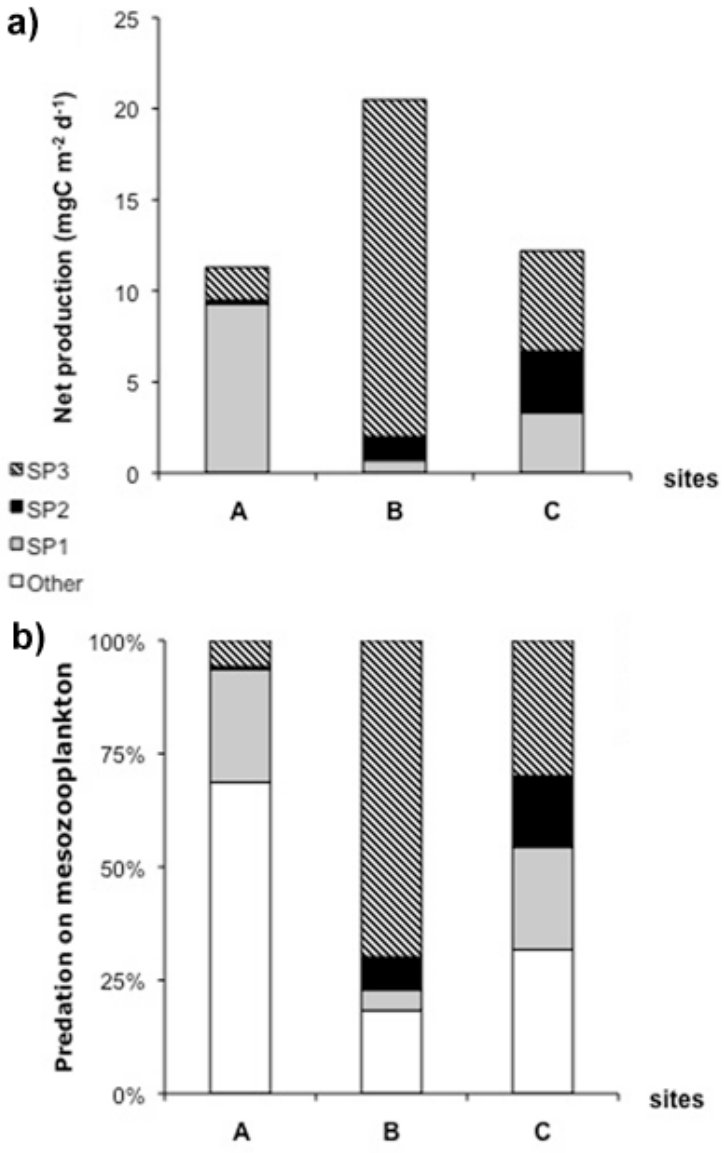
a)
Net production (mgC m-2 d-1)
25
20
15
10
5
0
SP3
SP2
SP1
Other
A
B
C
sites
b)
Predation on mesozooplankton
100%
75%
50%
25%
0%
A
B
C
sites

Fig. 4

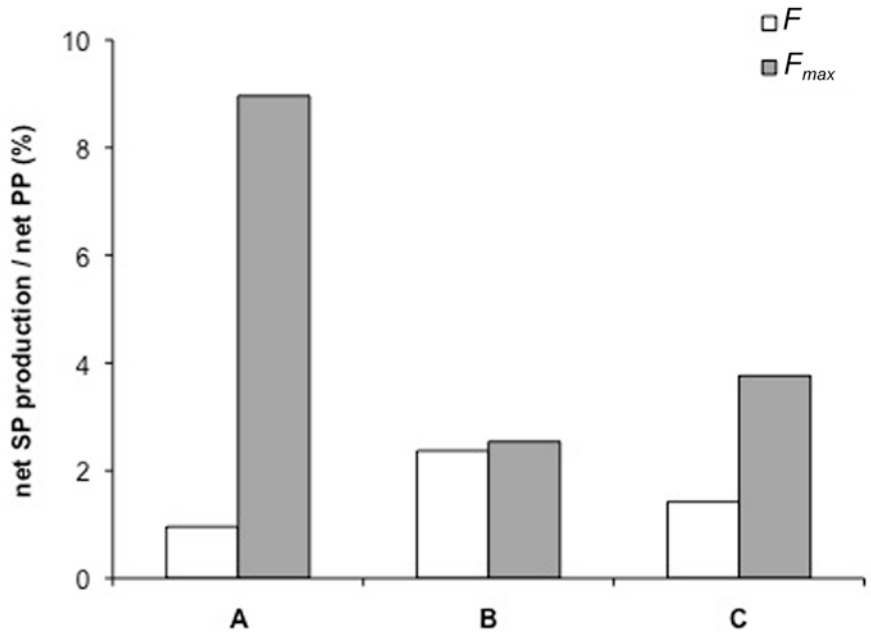

Fig. 5

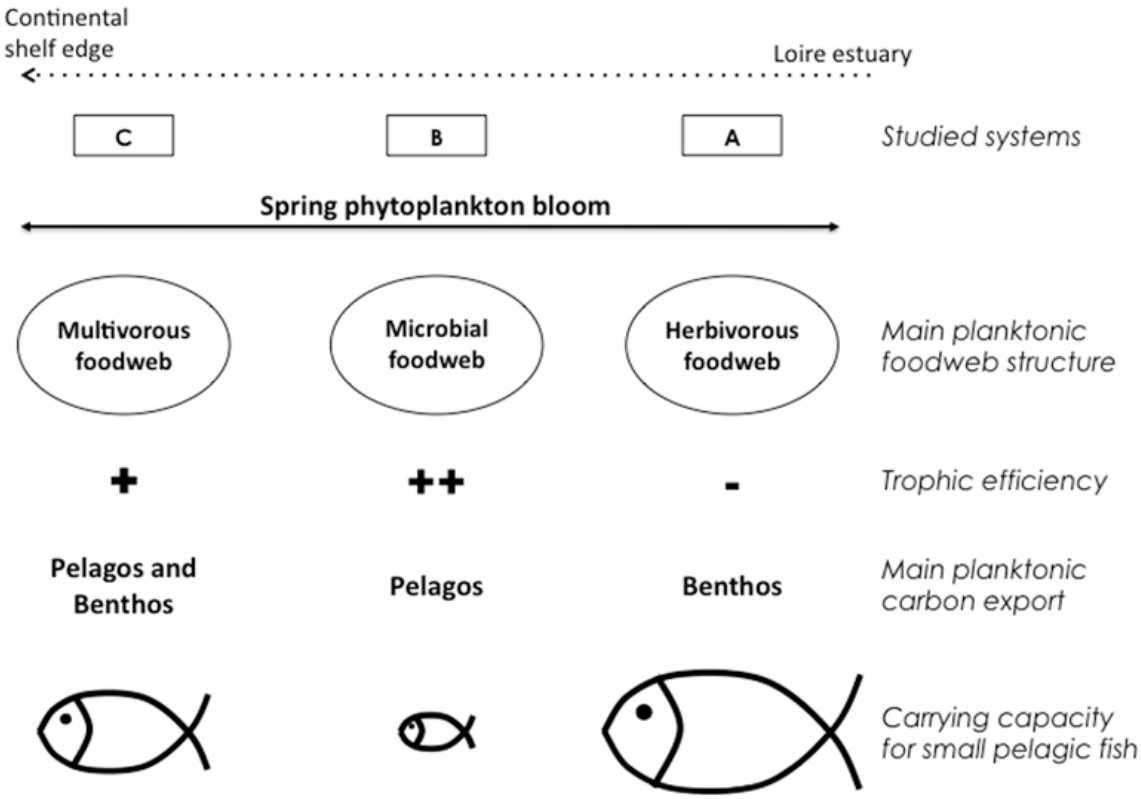
Continental shelf edge
Loire estuary
C
B
A
Studied systems
Spring phytoplankton bloom
Multivorous foodweb
Microbial foodweb
Herbivorous foodweb
Main planktonic foodweb structure
+
++
-
Trophic efficiency
Pelagos and Benthos
Pelagos
Benthos
Main planktonic carbon export
Carrying capacity for small pelagic fish

Fig. 6

Table 1: Production data (mgC m^{-2} d^{-1}) used as input values within the equality set and biomass data (mgC m^{-2}) used within the constraint set to build the three systems. Production formulations used symbols of carbon flows described in Table 2.

			A	B	C
Productions	**Picophytoplankton**	CgppTOph1 – 0,5 Cph1TOres	632.0	782.1	412.0
	Nanophytoplankton	CgppTOph2 – 0,5 Cph2TOres	217.5	287.9	444.5
	Microphytoplankton	CgppTOph3 – 0,5 Cph3TOres	737.1	21.7	197.7
	Bacteria	CbacTOpro + CbacTOdoc	50.6	37.8	66.7
Biomasses	**Bacteria**		137,0	173.1	201.4
	Protozoa		52.9	20.5	35.8
	Mesozooplankton		2517.0	1375.4	1669.3
	Small pelagic fish 1		1594.1	522.2	2375.6
	Small pelagic fish 2		94.1	770.3	2064.8
	Small prelagic fish 3		1296.5	13510.2	3691.5

Table 2: Flow formulations, descriptions and values (mgC m^{-2} d^{-1}) issued from direct measures (bold font) and from inverse analysis calculations (normal font).

Symbol	Description	A	B	C
CgppTOph1	Gross primary production of picophytoplankton	**743.6**	**806.6**	**450.7**
CgppTOph2	Gross primary production of nanophytoplankton	**255.9**	**295.3**	**455.9**
CgppTOph3	Gross primary production of microphytoplankton	**798.9**	**22.3**	**202.8**
Cph1TOres	Respiration by picophytoplankton	**223.1**	**48.8**	**77.5**
Cph1TOpro	Grazing of picophytoplankton by Protozoa	410.4	593.4	296.7
Cph1TOdoc	DOC excretion by picophytoplankton	110.2	164.3	76.4
Cph2TOres	Respiration by nanophytoplankton	**76.8**	**14.8**	**22.8**
Cph2TOpro	Grazing of nanophytoplankton by protozoa	0.0	0.0	58.9
Cph2TOmes	Grazing of nanophytoplankton by mesozooplankton	157.8	128.7	177.7
Cph2TOdet	Detritus production by nanophytoplankton	3.4	123.8	153.2
Cph2TOdoc	DOC excretion by nanophytoplankton	17.9	28.1	43.3
Cph3TOres	Respiration by microphytoplankton	**123.5**	**1.1**	**10.1**
Cph3TOpro	Grazing of microphytoplankton by protozoa	95.5	0.0	0.0
Cph3TOmes	Grazing of microphytoplankton by mesozooplankton	259.5	0.0	0.0
Cph3TOsp2	Grazing of microphytoplankton by small pelagic fish 2	1.4	7.9	32.3
Cph3TOdet	Detritus production by microphytoplankton	105.1	0.0	0.0
Cph3TOdoc	DOC excretion by microphytoplankton	67.5	2.1	19.3
Cph3TOlos	Sedimentation of microphytoplankton	146.3	11.2	141.1
CproTOres	Respiration by protozoa	306.1	156.5	222.4
CproTOmes	Grazing of protozoa by mesozooplankton	139.1	208.3	105.6
CproTOdet	Detritus production by protozoa	55.6	203.3	52.1
CproTOdoc	DOC excretion by heterotrophic protozoa	55.6	63.1	42.2
CmesTOres	Respiration by mesozooplankton	319.9	68.4	92.4
CmesTOsp1	Predation of mesozooplankton by small pelagic fish 1	44.4	6.3	28.0
CmesTOsp2	Predation of mesozooplankton by small pelagic fish 2	1.0	9.8	19.3
CmesTOsp3	Predation of mesozooplankton by small pelagic fish 3	10.3	95.5	36.8

Table 2 continued

Symbol	Description	A	B	C
CmesTOdet	Detritus production by mesozooplankton	142.2	102.6	61.6
CmesTOdoc	DOC excretion by mesozooplankton	71.1	34.2	30.8
CmesTOlos	Outflows of mesozooplankton by other predation	122.0	25.1	39.1
Csp1TOres	Respiration by small pelagic fish 1	30.7	4.4	21.9
Csp1TOdet	Feces production by small pelagic fish 1	4.4	1.3	2.8
Csp1TOlos	Outflows of small pelagic fish 1 by predation	9.3	0.0	0.0
Csp1TOsp3	Predation of small pelagic fish 1 by small pelagic fish 3	2.0	12.9	43.0
Csp2TOres	Respiration by small pelagic fish 2	0.2	3.5	5.2
Csp2TOdet	Feces production by small pelagic fish 2	0.2	0.0	0.0
Csp2TOlos	Outflows of small pelagic fish 2 by predation	21.4	108.9	49.7
Csp2TOsp3	Predation of small pelagic fish 2 by small pelagic fish 3	2.6	31.8	6.1
Csp3TOres	Respiration by small pelagic fish 3	1.8	18.5	5.5
Csp3TOdet	Feces production by small pelagic fish 3	15.5	61.7	17.8
Csp3TOlos	Outflows of small pelagic fish 3 by predation	0.0	0.7	3.3
CextTOsp3	Predation of other preys (fish. euphausiids) by small pelagic fish 3	0.0	1.3	3.4
CdocTObac	DOC absorption by bacteria	440.3	378.3	298.0
CbacTOres	Respiration by bacteria	389.7	340.5	231.3
CbacTOpro	Grazing of bacteria by protozoa	**50.6**	**37.8**	**66.7**
CbacTOdoc	DOC excretion by bacteria	**0.0**	**0.0**	**0.0**
CdetTOdoc	Detritus dissolution into DOC	117.9	86.5	86.0
CdetTOpro	Detritus consumption by protozoa	0.0	0.0	0.0
CdetTOmes	Detritus consumption by mesozooplankton	154.4	4.9	24.6
CdetTOlos	Outflows of detritus by sedimentation	41.2	374.9	170.3

Table 3: Limits of P/B and Q/B ratios (d^{-1}) used within the inequality set to build the three systems with small pelagic fish predation (P: production, B: biomass and Q: consumption). SP1: small pelagic fish 1, SP2: small pelagic fish 2, SP3: small pelagic fish 3.

		A	B	C
SP1	*Lower P/B*	0.0034	0.0008	0.0008
	Higher P/B	0.0058	0.0017	0.0014
	Lower Q/B	0.0223	0.0121	0.0118
	Higher Q/B	0.0287	0.0236	0.0197
SP2	*Lower P/B*	0.0011	0.0011	0.0011
	Higher P/B	0.0016	0.0016	0.0016
	Lower Q/B	0.0230	0.0230	0.0230
	Higher Q/B	0.0250	0.0250	0.0250
SP3	*Lower P/B*	0.0008	0.0008	0.0008
	Higher P/B	0.0014	0.0014	0.0015
	Lower Q/B	0.0118	0.0118	0.0118
	Higher Q/B	0.0199	0.0198	0.0215

Table 4: Systems characteristics with **ratios** (%) of net heterotrophic plankton production (bacteria -net BP-, protozoa -net Pro.P- and mesozooplankton -net Mes.P-) on net primary production (net PP); **Effective trophic level of mesozooplankton** and **Finn cycling index** (FCI, %).

	A	**B**	**C**
Net BP/net PP (%)	4.29	4.37	7.76
Net Pro.P/net PP (%)	11.80	24.08	12.28
Net Mes.P/net PP (%)	15.07	15.81	14.32
Effective trophic level of mesozooplankton	2.21	2.65	2.40
FCI (%)	7.77	4.96	7.95