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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 (PP) and the flux of biogenic carbon in the oceans are major issues in biological oceanography (Duarte and Cebrian, 1996). The fate of PP depends on the path carbon takes within planktonic foodwebs. Two simplified patterns, the grazing food chain and the microbial foodweb, have been distinguished based on the size of the main algal producers (Azam et al., 1983; Sommaruga, 1995). The most common view is that the planktonic foodweb exports biogenic carbon mainly during diatom blooms (Cushing, 1989; Legendre, 1990) when the algal cells are either grazed directly by metazoans or sink out of the photic zone (Legendre, 1990). This situation (upwelling, coastal waters) pertains to the most productive worldwide fisheries (Cushing, 1989). The opposite situation is found in oligotrophic waters, where the main primary producers are pico- and nanophytoplankton that are not grazed directly by mesozooplankton (Capriulo et al., 1991). Within that type of ecosystem, the biogenic carbon is recycled through the microbial foodweb before it reaches metazoans (Cushing, 1989; Legendre and Le Fevre, 1995). Such a planktonic foodweb structure supports the lowest rates of export of biogenic carbon (Legendre and Rassoulzadegan, 1996) and less productive fisheries. In terms of these two planktonic foodweb types, foodweb structure influences a system's capacity to support benthic and/or pelagic fish production (Sommer et al., 2002). Hence, describing the planktonic foodweb structure

and functioning is crucial to developing understanding of the trophic links between plankton communities and higher trophic levels.

In the Bay of Biscay, small pelagic (SP) fish such as anchovy or sardine are commercially important. In spring and early summer, the peak spawning period (May–July), they are mainly localized over the continental shelf (Motos et al., 1996). Previous studies have described winter diatom blooms on the continental shelf of the Bay of Biscay (Gohin et al., 2003) that lead to phosphorus limitation in early spring (Herbland et al., 1998). As a consequence, spring reflects a transient situation from a system dominated by large phytoplankton (from the winter diatom bloom) to one dominated by small phytoplankton, which are better competitors in phosphorus-limited conditions (Herbland et al., 1998). During spring, the planktonic foodweb in the Bay of Biscay is based on multivorous trophic flows (Legendre and Rassoulzadegan, 1995). The consequences of these planktonic foodweb 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 greater control over relative carbon export than phytoplankton size structure. Here, we focused on examining the export to the higher pelagic foodweb (F; Legendre and Rivkin, 2002), and specifically on

production of the SP fish that are important economically in the area. The method of inverse analysis (Vézina and Platt, 1988; Vézina, 1989) was used to reconstruct the entire foodweb, combining plankton and fish compartments, and to estimate carbon flows.

The overall goal of the study was to specify the relationship between planktonic foodweb functioning and the system's capacity to export biogenic carbon to SP fish (F) during spring. We investigated two estimates of export to higher pelagic levels: (i) export consistent with the available data on fish abundance, and (ii) potential export, i.e. the maximum carbon flux that can support pelagic fish production given constraints on PP and foodweb structure (F_{max}). The question posed was whether there is a substantial gap between the two estimates and whether foodweb structure influences the d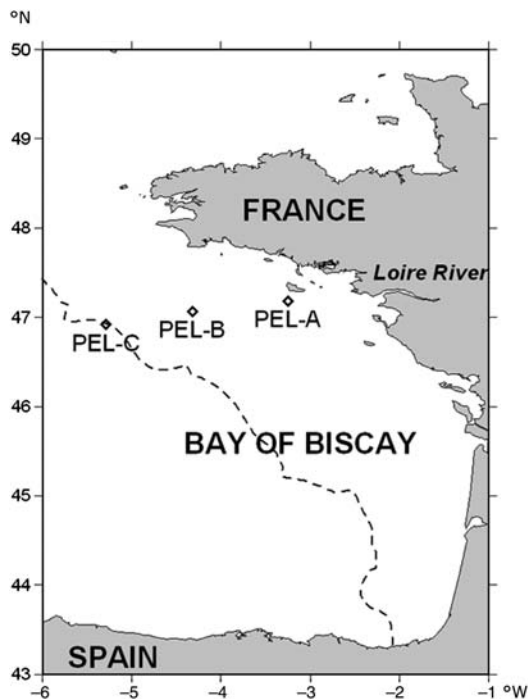ifference between real export and export capacity. As far as we are aware, this is the first time that inverse analysis has been used to investigate the productive capacity of fisheries ecosystems.

Material and methods

The Bay of Biscay (Figure 1) is an open bay within the eastern Atlantic, with a continental shelf up to 200 km wide. Data for the study were obtained from the PEL2001 oceanographic cruise (Figure 1) of spring 2001. Plankton was sampled at three stations (A, 47°11′N 3°15′W, 70 m deep on 11 May 2001; B, 47°04′N 4°19′W, 129 m deep on 12 May 2001; and C, 46°55′N 05°17′W, 381 m deep on 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 offshore; Figure 1). Based on the data available from the three stations, three foodwebs were constructed using inverse analysis.

Plankton and fish data

Data representing planktonic ecosystems, i.e. production and biomass (Table 1), were sourced from Marquis et al. (2007). In terms of the variation in field-data estimation over a 1-week survey (Biomet cruises; cf. Marquis et al., 2007), the overall error estimated for plankton input data was assumed to be <20%. Before comparing the three systems, the impact of this uncertainty in the input data on the estimates of carbon flow was tested with a sensitivity analysis in which each input datum was individually changed by plus and minus 20% (cf. Marquis et al., 2007).

The SP 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*). The fish species were regrouped into functional compartments based on their 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). The three groups were:

(i) small pelagic 1 (SP1)—strictly zoophagous (anchovy, sprat, small horse mackerel ≤16 cm, small sardine ≤18 cm, and small Atlantic and chub mackerel ≤24 cm);

(ii) small pelagic 2 (SP2)—phytozoophagous (large sardine >18 cm); and

Figure 1. Map of the Bay of Biscay showing the three stations of the study: PEL-A is station A, PEL-B is station B, and PEL-C is station C. The dashed line shows the approximate extent of the French continental shelf.

Table 1. Production data used as input values within the equality set and biomass data used within the constraint set to build the three systems.

Parameter	Group		Station A	Station B	Station C
Production (mgC m^{-2} d^{-1})	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
Biomass (mgC m^{-2})	Bacteria		137.0	173.1	201.4
	Protozoa		52.9	20.5	35.8
	Mesozooplankton		2 517.0	1 375.4	1 669.3
	Small pelagic fish 1		1 594.1	522.2	2 375.6
	Small pelagic fish 2		94.1	770.3	2 064.8
	Small pelagic fish 3		1 296.5	13 510.2	3 691.5

The production formulations use the symbols of carbon flows described later in Table 2.

(iii) small pelagic 3 (SP3)—meso- and macrozoophagous and ichthyophagous (large horse mackerel >16 cm and large Atlantic and chub mackerel >24 cm).

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

Construction and analysis of foodwebs

Inverse analysis is a numerical method for developing complete, steady-state foodweb models (Vézina and Platt, 1988; Vézina, 1989). An *a priori* linear model (Figure 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 to build the best estimates of foodweb flows. The solution selected is the minimum of a norm (the parsimony principle). A complete description of the method is given in Marquis *et al.* (2007), and the algorithm of resolution from Vézina and Platt (1988) was programmed by G. A. Jackson using Matlab© software.

In the work reported here, the method used in Marquis *et al.* (2007) was subjected to two modifications concerning (i) the coupling of the SP fish compartments with the plankton ecosystems, and (ii) estimating the carrying capacity.

Coupling fish compartments with plankton ecosystems

We used concurrent data on fish abundance to constrain the flow from plankton to higher consumers. This is something that is done rarely, if ever, in inverse analysis, in which 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 SP fish compartments (Figure 2). The new *a priori* model included 50 average flows of carbon under 1 m^2 of the photic zone during 1 d (Table 2).

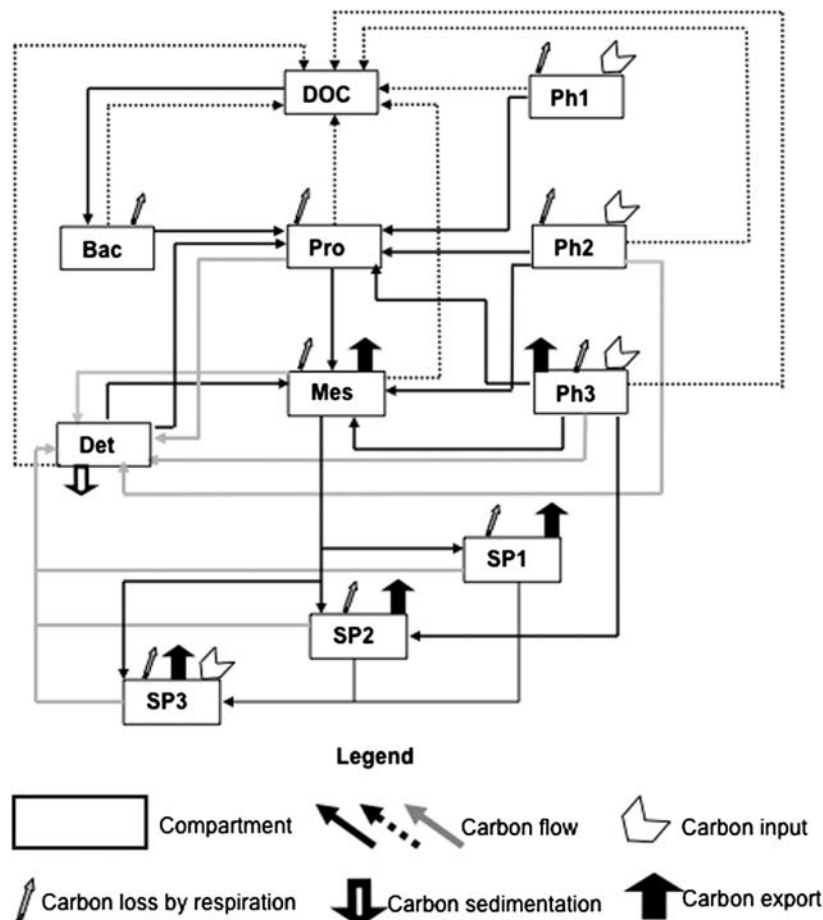**Figure 2.** An *a priori* model used to build the coupled SP fish/plankton systems. The abbreviations are Ph1, picophytoplankton (<2 μm); Ph2, nanophytoplankton (2–20 μm); Ph3, microphytoplankton (>20 μm), Bac, bacteria; Pro, protozoa (ciliates and flagellates, 20–200 μm); Mes, mesozooplankton (>200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

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

Symbol	Description	Station A	Station B	Station C
CgppTOph1	Gross PP of picophytoplankton	**743.6**	**806.6**	**450.7**
CgppTOph2	Gross PP of nanophytoplankton	**255.9**	**295.3**	**455.9**
CgppTOph3	Gross PP 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	Dissolved organic carbon 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	Dissolved organic carbon 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	Dissolved organic carbon 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	Dissolved organic carbon 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
CmesTOdet	Detritus production by mesozooplankton	142.2	102.6	61.6
CmesTOdoc	Dissolved organic carbon 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	Faeces 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	Faeces 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	Faeces 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 prey (fish, euphausiids) by small pelagic fish 3	0.0	1.3	3.4
CdocTObac	Dissolved organic carbon 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	Dissolved organic carbon excretion by bacteria	0.0	0.0	0.0
CdetTOdoc	Detritus dissolution into dissolved organic carbon	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

The 22 inequalities concerning fish compartments described their consumption (Q) and production (P) and were calculated with the mean ratios of consumption on biomass (Q/B) and production on biomass (P/B) of each SP fish group (Table 3). The highest and the lowest values of the 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. Egestion (faeces production) flux ranged between 10 and 20% of consumption (after Klumb, 2002). The diet of SP2 and SP3 fish was assumed to consist of between 40 and 60% mesozooplankton and that of SP1 fish of 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 fish 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

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; Q, consumption; SP1, small pelagic fish 1; SP2, small pelagic fish 2; SP3, small pelagic fish 3).

Fish group	Parameter	Station A	Station B	Station 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

correspond to diet of euphausiids (derived from the rate of euphausiid ingestion estimated in Sanchez and Olaso, 2004).

Estimating carrying capacity

We used linear inverse modelling 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 (Luenberger, 1984) to calculate F_{max}, the potential carbon export. The goal of this carrying-capacity analysis was to obtain the theoretical maximum production of SP fish supported by each of the three planktonic foodwebs. To simplify the analysis, just one fish compartment production was maximized directly, whereas the other two increased in relation to its maximization. The ratios between production and consumption of each fish compartment were also preserved in estimating the carrying capacity. The results of the inverse analyses were used to fix the P/Q ratio of each SP compartment and the ratios of SP1 and SP2 production to SP3 production. Then, the linear programming was applied to maximize SP3 production. Linear programming produces the highest value of SP production (F_{max}) 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 modelled foodweb. Here, 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 foodweb 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 foodweb.

Results
Foodweb functioning
Plankton

Total net production of the three size classes of phytoplankton (Figure 3) was high at the three stations, but total net PP 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 at stations B and C (98 and 80% of total net PP, respectively) and relatively lower at A (48% of total net PP).
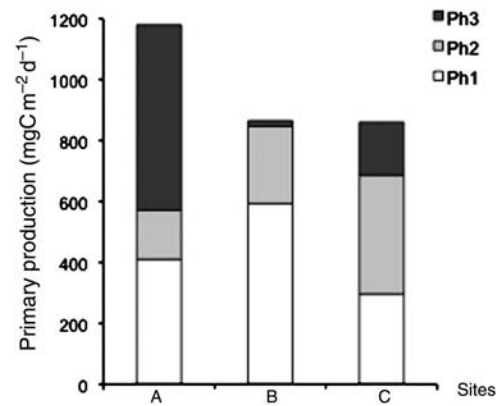

Figure 3. Contribution of the three phytoplankton size classes to net total PP (mgC m^{-2} d^{-1}) for the three foodweb systems. Ph1, picophytoplankton; Ph2, nanophytoplankton; Ph3, microphytoplankton.

Net bacterial production was low at the three stations and represented <8% of total net PP (Table 4). The net protozoan production as a proportion of total net production was similar at A and C, but twice as high at B (Table 4). Mesozooplankton production constituted similar proportions of total PP in the three foodwebs (Table 4). Because of the stronger role of protozoa within the diet of mesozooplankton, the mesozooplankton effective trophic level was highest at the midshelf station (2.65; Table 4).

The FCI (Table 4) revealed that the foodwebs at stations A and C had more significant cycling pathways than that at station B, i.e. the quantity of carbon flowing through the dissolved organic carbon and detritus compartments was higher at A and C than at B (Table 4).

Pelagic fish

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

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

Export to pelagic fish and carrying capacity

In terms of export (F), station B had the highest ratio of total net SP production to total net PP (2.4%; Figure 5), and station A had

Table 4. System characteristics, with ratios (%) of net heterotrophic plankton production [bacteria (net BP), protozoa (net Pro.P), and mesozooplankton (net Mes.P)] on net PP, and values of effective trophic level of mesozooplankton and of the FCI.

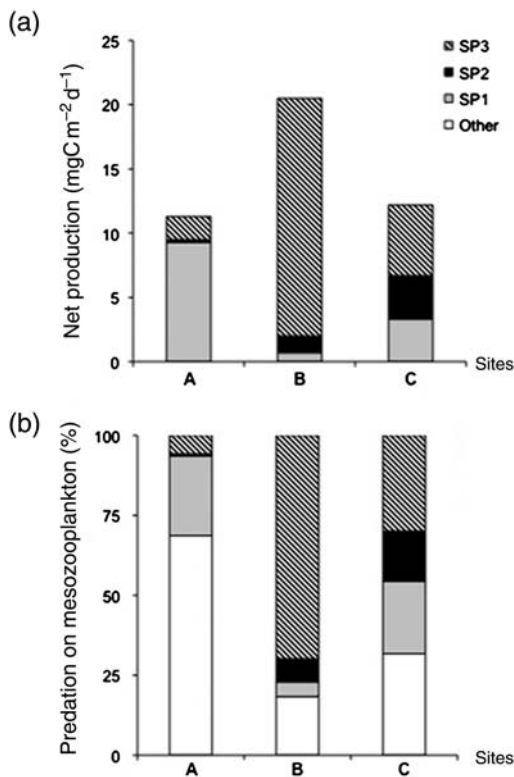| Ratio/value	Station A	Station B	Station C
Net BP/net PP (%)	4.29	4.37	7.76
Net Pro.P/net PP (%)	11.80	24.08	12.28
Net Mes.P/net PP (%)	15.07	15.81	14.32
Effective trophic level of mesozooplankton	2.21	2.65	2.40
FCI (%)	7.77	4.96	7.95

Figure 4. (a) Contribution of each compartment of SP fish to total fish production (in mgC m^{-2} d^{-1}), and (b) the fate of carbon outflow from mesozooplankton in percentage of total predation on mesozooplankton: 177.7, 136.8, and 123.2 mgC m^{-2} d^{-1}, respectively, at sites A, B, and C. SP1, small pelagic fish 1 (strictly zoophagous: anchovy, sprat, small horse mackerel <16 cm, and small sardine <18 cm); SP2, small pelagic fish 2 (phytozoophagous: large sardine >18 cm); SP3, small pelagic fish 3 (meso-macrozoophagous and ichthyophagous: large horse mackerel >16 cm and Atlantic and chub mackerel); Other, other predators of mesozooplankton (euphausiids, larger fish, etc.).

Figure 5. Ratios of total SP fish production to total net PP (%): export (F) and capacity (F_{max}) for the three foodweb systems.

sedimentation and other predation on mesozooplankton, whereas the sedimentation of detritus increased as a consequence of higher mesozooplankton ingestion (detritus mainly composed of faecal pellets).

Discussion

Planktonic foodweb functioning

Net PP was high at the three stations (>800 mgC m^{-2} d^{-1}), corresponding to values typical of the 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 PP ratios were very low, as also observed during spring in the upwelling coastal area off the coast of northern Spain (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 arise first near the coast or river mouths (stratification associated with low salinity, combined with relatively high nutrient levels) before moving offshore (Yin et al., 1996). However, in our study, the microphytoplankton bloom seems to have been less advanced inshore than midshelf (station B is located 60 nautical miles farther offshore than station A). This observation is consistent with satellite observations (Gohin et al., 2003) in which the spring bloom appears in the middle of the continental shelf before it does in coastal areas. This situation may be due to the turbidity of river plume waters. The resulting low light environment attributable to riverine discharge may have delayed the inshore bloom (Iriarte and Purdie, 2004).

As shown in Marquis et al. (2007), sensitivity analysis, carried out by changing the input data by ±20%, revealed that the inverse solutions clearly separated out the three models based on their different flow structure. Therefore, combining the observations on bloom timing with those on microbial flows in each foodweb resulted in the description of three distinct states of functioning: the inshore station was dominated by direct trophic pathways (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, and the midshelf station represented an intermediate situation between a foodweb dominated by direct pathways to one dominated by microbial pathways (Legendre and Rassoulzadegan, 1995; Marquis et al., 2007).

the lowest value (1.0%). The difference between export (F) and capacity (F_{max}) was highest at station A (1.0–9.0%; Figure 5). The two values (F and F_{max}) were similar at station B (2.4 and 2.5%; Figure 5), but at station C the capacity was almost three times higher than the export (1.4–3.8%; Figure 5). In all three systems, as a consequence of constraining predation fluxes at their maximum limits, linear programming led to a considerable decrease (reaching virtually zero) in microphytoplankton
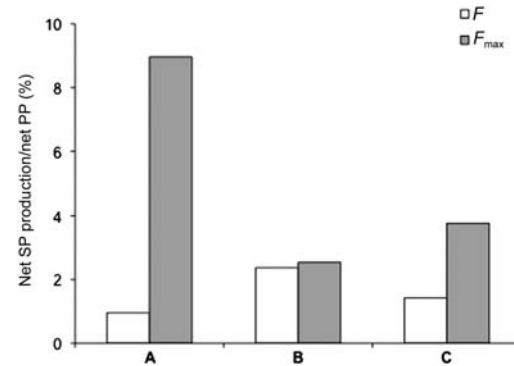
Predation on mesozooplankton

The differences in fish production observed among the three stations were related to fish biomass. As the three fish compartments showed similar ranges of P/B and Q/B ratios (Table 3), the spatial distributions of each fish species had an effect on the values of total pelagic fish production calculated for each station. During spring 2001, large sardine (SP2) were distributed along the shelf break, as they were 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 mackerel (SP3) were mainly distributed midshelf. Therefore, the highest production observed midshelf was related to the very large biomass of SP3 fish (>10 gC m^{-2}), attributable to the abundance there of mackerel.

However, the method used to obtain fish biomass data, combining acoustic surveys and trawl observations may induce an error in the estimate (Petitgas *et al.*, 2003). To assess whether there was a relationship between fish biomass estimation error and carbon-flow calculation, we tested the three fish biomasses individually at each station (results not shown). We did not explore effects of combined errors between them, but changed the selected biomass by $\pm10\%$ (the error margin considered for the fish biomass estimation) and re-ran the inverse analysis. The resulting carbon flows within the planktonic foodweb did not differ from the original values by $>10\%$, so we conclude that the uncertainty in fish biomass data will have had little effect on the final differences between F and F_{max} resulting from our analysis when comparing each foodweb.

The spring conditions of the three foodwebs may have allowed a large export of carbon to planktivorous fish because PP attained high levels, and planktonic grazers (protozoa and mesozooplankton) were present in the three foodwebs (Legendre and Rassoulzadegan, 1996; Marquis *et al.*, 2007). The flow of carbon available to planktivores was sufficient in the three foodwebs to cover the food requirements of the SP fish present. In fact, SP fish did not appear to be the most important predator of mesozooplankton inshore (30% of the total predation on mesozooplankton), though they took between 60 and 65% of the total predation on mesozooplankton at the midshelf and the shelf-edge stations, respectively. This relatively low level of predation on mesozooplankton inshore suggests that a large fraction of the mesozooplankton production there may be available for other planktivorous organisms, such as suprabenthic zooplankton (euphausiids and mysids) or macrozooplankton (medusae or large tunicates). The observations made on the biomass and diet of such macrozooplankton in the area close to the Bay of Biscay may confirm this result of the inverse analysis. For instance, macrozooplankton biomass is high during spring in areas close to the Bay of Biscay, such as St Brieuc Bay (Vallet and Dauvin, 1999) and the biomass is dominated by mysids. In the Baltic Sea, the diet of mysids consists of a large proportion of copepods and rotifers throughout the year (Rudstam *et al.*, 1992), and euphausiids of the Northeast Atlantic are important predators of copepods (Båmstedt and Karlson, 1998). Moreover, along the Cantabrian coast, mysids and euphausiids consume ~60% of the total carbon available from mesozooplankton over a year (Sanchez and Olaso, 2004). Despite the importance of mysid and euphausiid populations (as well as other possible planktivorous fish) in the pelagic foodweb of the Bay of Biscay, as revealed by our model, the distribution and the biomass of those predators

have never been as intensively studied as those of SP fish. From our model results, we believe 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 PP to pelagic fish

The export to pelagic fish (F) corresponded to the relative fish production (ratio of net pelagic fish production to net PP) and varied between 1 and 2.4% in the three foodwebs. The value of 2.4% found midshelf seemed high compared with 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 foodweb, as generally assumed, it would mean that fish production would not exceed 1% of PP. Indeed, the trophic level of SP fish may change with planktonic foodweb structure, and the resulting relative fish production may be $>1\%$ of PP (in upwelling areas; Ryther, 1969), or far lower (Iverson, 1990). In our study, the high value of relative fish production found midshelf means that the trophic efficiency between each trophic level in the foodweb was $>10\%$ (Sommer *et al.*, 2002). Such a high trophic efficiency might have been the result of tight coupling between trophic levels (Gaedke and Straile, 1994). Those authors stated that this situation would arise if PP was nutrient-limited and microbial pathways dominated carbon pathways in the planktonic foodweb. Such situations can be observed at station B, where the immediately preceding microphytoplankton bloom led to nutrient limitation and the production of picophytoplankonic cells supporting active protozoan grazing (relatively high production of protozoa; Table 4). This hypothesis is reinforced by the very low FCI value measured midshelf (Table 4), which shows very little recycling activity despite the importance of microbial communities (protozoa). Moreover, we argue that predation control on mesozooplankton by the very large population of planktivorous fish at that site (SP3) may have enhanced the tight coupling at lower trophic levels and hence the final trophic efficiency of the planktonic foodweb.

Support of benthic and pelagic production

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

On the other hand, the gap between export to pelagic fish (F) and carrying capacity (F_{max}) was very different between the three stations, with the greatest difference inshore and the least difference midshelf. These dissimilarities may be related to the distinctive foodweb structures (Figure 6). The *in situ* conditions at the inshore station led to the export of large quantities of carbon, mainly through the sedimentation of fresh microphytoplankton cells and detritus. When maximizing pelagic fish predation, those carbon flows were reduced and the corresponding carbon was transferred towards fish, resulting in a very high carrying capacity. Cushing (1989) and Legendre (1990) both concluded that microphytoplankton blooms allowed the greatest export of carbon. They also noted that areas with microphytoplankton blooms sustained the largest fisheries, but that the relatively low
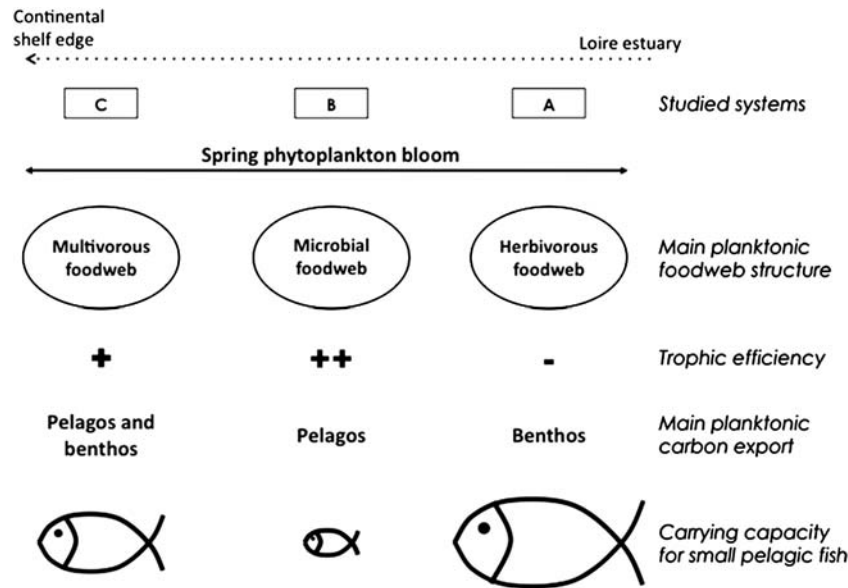
Figure 6. A schematic synthesis of the results, with emphasis on the carbon export to fish populations, with F being the main planktonic carbon export and F_{max} the carrying capacity of small pelagic fish.

export to pelagic fish of the inshore foodweb demonstrated that a microphytoplankton-based foodweb was not optimal for strictly pelagic fish production. We therefore argue that the inshore foodweb seemed configured to support demersal and benthic production (Figure 6) through the downward export of detritus and microphytoplankton aggregates (Richardson et al., 2000). However, because of the relatively shallowness of the inshore station, pelagic fish should have been be able to consume descending particles. This possibility is not included in the present model, but it does need to be taken into account in future work, to confirm the proportion of the spring-bloom production actually reaching the benthos in the inshore foodweb.

Midshelf, PP was almost exclusively exported to pelagic fish production, and the general trophic efficiency was high. The capacity (F_{max}) of the midshelf station was equivalent to the export (F), meaning that the maximum level of pelagic fish production supported was reached under in situ conditions. Despite the low biomass observed, the protozoan community was very active in this foodweb in response to the importance of the pico-phytoplanktonic production (Legendre and Rassoulzadegan, 1996). As in the example of Northeast Water Polynya (Pesant et al., 2000), the downward export of carbon was low in this plank-tonic foodweb, which was dominated by small phytoplankton. Downward carbon flux may still exist through the sedimentation of copepod faecal pellets, but such pellets may not sink as fast as diatom aggregates and hence may not be a direct energy source for benthic metazoans (Legendre and Rivkin, 2002). As a conse-quence of these low sedimentation flows, the picophytoplankton-based foodweb showed the highest export (F) of carbon to pelagic fish, but the lowest carrying capacity (F_{max}; Figure 6). Therefore, the picophytoplankton-based foodweb with high protozoan activity emerged as the optimal situation in support of pelagic fish production. Finally, the shelf-edge foodweb that included both microbial and herbivorous pathways was an intermediate situation between the two extremes (inshore and midshelf), with intermediate carrying capacity (F_{max}) and an intermediate gap between F and F_{max} (Figure 6). Pelagic and benthic production

was then supported in the in situ conditions of that multivorous foodweb.

Conclusions

The three situations (stations) illustrated the complexity of the existing relationships between planktonic foodwebs and carbon export in the ocean (Legendre and Rassoulzadegan, 1996). With equivalent levels of PP, the three foodwebs differed from each other through the number of steps existing between PP and plank-tivorous fish and through the capacity to support both pelagic and benthic production. In Marquis et al. (2007), analysis of simple plankton foodwebs led to the conclusion that the total carbon available to pelagic predators was less controlled by the size struc-ture of the primary producers than by the bacterial to PP ratio. In the current study, although this conclusion is confirmed, the main primary producer size and foodweb functioning were directly influencing the carrying capacity of the planktonic foodweb 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 primary producers nor planktonic foodweb functioning (Iverson, 1990). From the results of this study, however, we argue that a distinction between the quantities of carbon available, the carbon flows to pelagic fish, and the carrying capacity of the ecosystem needs to be carefully drawn and that plankton foodweb functioning should not be neglected in future fisheries studies.

Acknowledgements

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