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Fish ecology and terrestrial carbon use in coastal areas: implications for marine fish production

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Summary

1. To investigate the role of fish ecology in controlling terrestrial particulate organic matter (POM) uptake by benthic fish species and population responses to changes in continental inputs to coastal areas, depth distribution, diet and stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) data from the juveniles and adults of five important flatfish species (*Arnoglossus laterna*, *Buglossidium luteum*, *Citharus linguatula*, *Solea lascaris* and *S. solea*) were compared off the Rhone River delta (NW Mediterranean).

2. In moderate river discharge, isotopic signatures differed with fish species and benthic life stage, suggesting intra- and interspecific differences in trophic levels and food sources. Food web analysis indicated terrestrial POM uptake in all life stages of *S. solea* and *A. laterna* ($\delta^{13}\text{C} = -20.1$ to -20.0‰ and -18.9 to -18.2‰ , respectively), in the adults of *B. luteum* ($\delta^{13}\text{C} = -19.0\text{‰}$) and in the juveniles of *S. lascaris* ($\delta^{13}\text{C} = -18.7\text{‰}$), whereas all life stages of *C. linguatula* ($\delta^{13}\text{C} = -17.6\text{‰}$), *S. lascaris* adults ($\delta^{13}\text{C} = -16.9\text{‰}$) and *B. luteum* juveniles ($\delta^{13}\text{C} = -17.5\text{‰}$) exploited marine POM almost exclusively.

3. Fish diet and depth distribution accounted fully for the intra- and interspecific differences in terrestrial POM uptake observed. Greater terrestrial signatures were observed in fish eating larger quantities of deposit-feeding polychaetes (the main prey exploiting terrestrial POM for growth) and occurring mainly in the 30–50 m depth zone (where river POM sedimentation and its uptake by the benthos were the highest). Due to intra- and interspecific differences in fish depth distribution and diet, Rhone River floods were predicted to have little effect on *C. linguatula* populations but to increase the other four species' local stocks for several years, with a maximum impact on *S. solea*.

4. This study shows that the ability of benthic fish to exploit terrestrial POM inputs to the coastal zone depends strongly on their ecology. As this parameter will determine fish populations' reactions to river floods, it must be assessed carefully before making hypotheses about the consequences of variations in river discharge on coastal fisheries' production.

Key-words: benthic food webs, flatfish, population dynamics, river run-off, stable isotopes.

Introduction

Successful fisheries management depends on our ability to identify and explain causes of population fluctuations and changes. Relationships between climatic change and modification of fisheries have been explained for some pelagic species (Cushing 1982, 1995; Yañez, Garcia & Barbieri 1998). However, the effects of large and irregular

year-to-year variations in environmental parameters induced by weather conditions on demersal fish resources are less well understood (Salen-Picard *et al.* 2002). Temperature and fluctuation in planktonic primary productivity have been the main environmental factors studied (Nielsen & Richardson 1996), but less attention has been paid to the effects of fluctuations in macrobenthic communities as fish food resources.

Land-based run-off has for long been thought to enhance demersal fishery production in various coastal areas where fish abundance follows river discharge variations (Kerr & Ryder 1992; Cushing 1995; Lloret *et al.* 2001). This link has been attributed mainly to enhanced planktonic production by river nutrient loads

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(Cushing 1982; Nielsen & Richardson 1996; Maslowski 2003). However, efficient exploitation of river-borne particulate organic matter (POM) by some marine benthic organisms has been shown recently (Bouillon *et al.* 2000; Darnaude *et al.* 2004b), with active uptake by coastal benthic food webs sustaining demersal fish (Darnaude *et al.* 2004a). As terrestrial POM is brought to the sea mainly during river floods, this explains the link between river discharge and local production of certain demersal fish (Salen-Picard & Arlhac 2002; Salen-Picard *et al.* 2002).

However, the potential of river floods to enhance multispecies demersal fisheries, which will vary according to fish ecology during benthic life (Salen-Picard *et al.* 2002), still needs to be assessed. Our previous work has shown that dietary differences explain most of the interspecific differences in terrestrial POM uptake by fish (Darnaude *et al.* 2004a). Because terrestrial POM use by marine macrobenthos varies according to availability in the environment, terrestrial POM transfer to demersal fish is also likely to depend on their distribution, due to spatial differences in terrestrial POM deposition in the coastal zone (Darnaude *et al.* 2004b). In the present study, carbon and nitrogen stable isotopes were used to assess intra- (juveniles vs. adults) and interspecific variations in terrestrial POM uptake in the five main flatfish (*Arnoglossus laterna*, *Buglossidium luteum*, *Citharus linguatula*, *Solea lascaris* and *Solea solea*) present off the Rhone River delta (NW Mediterranean). To assess the conditions for fish exploitation of terrestrial POM during juvenile and adult stages, these data were compared with diet and depth distribution data obtained from the same fish. Stable isotopes were then used to describe coastal benthic food webs within fish depth ranges of life. Provided that distinct isotopic signatures can be identified for the primary producers, stable isotopes constitute a powerful tool for the assessment of the main organic matter source(s) that sustain animal feeding (Vander Zanden & Rasmussen 2001). When combined, carbon and nitrogen stable isotopes allow the description of food web structure and organic matter transfer within animal communities (Kaehler, Pakhamov & McQuaid 2000; Polunin *et al.* 2001; Takai *et al.* 2002). The carbon isotope signature ($\delta^{13}\text{C}$), which increases from prey to predator by only 1–2‰, provides clues about the origin of the consumers' food (De Niro & Epstein 1978; Wada, Mizutani & Minagawa 1991), whereas the nitrogen signature ($\delta^{15}\text{N}$), which increases by 2.5–4.5‰ from food to consumer, helps define the organisms' trophic levels (Minagawa & Wada 1984; Post 2002). The assessment of the role of fish ecology in determining the consequences of terrestrial POM inputs on fish growth and reproduction is necessary in order to predict benthic fisheries responses to changes in river discharge.

MATERIALS AND METHODS STUDY AREA

This study was performed on the coastal soft bottoms located seawards of the Rhone River delta (43°14'–

43°22' N, 4°54'–5°03' E). The Rhone River is the most important run-off to the Mediterranean. Its inputs in nutrients play a key role in enhancing NW Mediterranean's productivity. However, they are relatively constant from year to year (Lochet & Leveau 1990), whereas terrestrial POM inputs by the river follow its discharge (Pont 1997; Sempéré *et al.* 2000). Terrestrial POM forms the major portion of terrestrial matter brought to the sea during river floods. On average, 6.2×10^6 t year⁻¹ of terrestrial particulate material is discharged in the river prodelta (Zuo *et al.* 1997). In this area, macro- and microphyto-benthic productions are low (Bodoy & Plante-Cuny 1980). Marine phytoplankton and Rhone River POM are the main sources of organic matter for benthic ecosystems (Cauwet *et al.* 1990; Darnaude *et al.* 2004a). More than 50% of sediment organic matter is of terrestrial origin irrespective of depth, but terrestrial POM sedimentation and availability are maximal at 30–50 m (Bouloubassi *et al.* 1997; Darnaude *et al.* 2004b). Sediment type and benthic community composition differ mainly between 0 and 20 m (sandy bottoms with a dominance of molluscs and polychaetes) and 30–100 m (muddy bottoms with polychaete-dominated communities) (Darnaude *et al.* 2004b). Flatfish are abundant throughout, and consist mainly of Soleidae (*S. solea*, *S. lascaris* and *B. luteum*), Bothidae (mainly *A. laterna*) and Citharidae (*C. linguatula*).

SAMPLING

Samples were collected during 2000–01, at the end of a 4-year period of moderate discharge for the Rhone River (Darnaude 2003). Juvenile and adult flatfish and their main prey were collected seasonally (winter, spring, summer) within three depth ranges (0–20 m, 30–50 m and 70–100 m) that reflect the main types of benthic environments occupied by the fish. To limit sampling-linked biases in fish distribution, diet and size, fish were collected over 24-h cycles of trawling (hauls of 30 min duration at 2 knots speed at 2-h intervals). Both a small commercial otter trawl targeting adult fish (swept area = 4 × 3 m; cod end mesh size = 20 mm) and a small experimental beam-trawl targeting juvenile fish (swept area = 1.5 × 0.5 m; cod end mesh size = 8 mm) were employed. Fish were counted and their total lengths recorded to assess juvenile and adult bathymetric distribution for each species. Fish guts were removed and preserved in 10% neutralized formaldehyde solution for stomach content analysis, and dorsal white muscle samples were taken for isotope analysis. Macrobenthic preys were collected using a pneumatic suction-sampler at 0–5 m depth by SCUBA diving and using a Smith–McIntyre grab at greater depths (10–20, 30–50 and 70–100 m). Macrobenthos samples were kept alive in filtered water from the sampling site for 24 h to allow gut evacuation. They were then sorted by taxon (mainly to the class or order level) under a binocular microscope and stored separately, after dissection of large individuals to remove hard parts and digestive tracts. At this stage, polychaetes were determined to species level to allow sorting them

by trophic group (Fauchald & Jumars 1979). Samples for isotope analysis were kept frozen before being processed. Rhone River POM and offshore seawater POM (marine phytoplankton) were chosen as proxies of the terrestrial and marine POM supplies to the benthic ecosystems studied. They were sampled in winter, spring and summer, i.e. during the main periods of high and low flow of the river (Sempéré *et al.* 2000), to ensure obtaining mean values that reflected seasonal variability in their isotopic signatures. For each season, Rhone River water samples were collected 6 km upstream of the river mouth. Seawater was sampled in the Gulf of Marseilles, outside the Rhone River influence (Frioul island: 43°15' N, 5°18' E; salinity > 37.8). Water samples were prefiltered on 250 µm-mesh sieves to remove zooplankton and detritus. POM samples (three per site per season) were obtained by filtering the corresponding water samples (3 × 20 L per site per season) on previously combusted and weighted Whatman GF/F glass fibre filters. Samples were kept frozen prior to stable isotope analysis.

FISH DIETS

Global (annual) diets of juvenile and adult *A. laterna*, *B. luteum*, *C. linguatula*, *S. lascaris* and *S. solea* were determined from the stomach contents of at least 30 individuals (≥ 10 per season) per species, life stage and depth. Prey items were identified and counted under a binocular microscope, following the procedure described in Darnaude, Harmelin-Vivien & Salen-Picard (2001). They were sorted down to the class or order level, with the exception of polychaetes, which were identified to species and pooled by trophic group following Fauchald & Jumars (1979). Prey category dry weights were recorded after 24 h drying at 45 °C. They were used to calculate prey weight percentages in flatfish diet (W%) at each depth.

STABLE ISOTOPE ANALYSIS

All samples were freeze-dried. Water POM samples (on GF/F filters) were cut into small pieces. Prey and fish samples were ground into a fine powder (< 60 µm) using a mortar and pestle. For small prey, several individuals were pooled and homogenized together to obtain enough material for analysis. Samples from large invertebrates (polychaete and mollusc soft tissues) and fish (white muscle) were analysed without any prior treatment. Samples of water POM and small invertebrates (bivalve juveniles, crustaceans, ophiuroids, etc.) were divided into two subsamples. The subsample for carbon isotope analysis was acidified with 1% HCl solution to remove carbonates (they present higher δ¹³C values than organic carbon; De Niro & Epstein 1978), rinsed with distilled water and oven-dried at 40 °C for 24 h. The nitrogen isotope analysis subsample was not acidified, as acidification modifies δ¹⁵N (Pinnegar & Polunin 1999). Three prey category samples and 10 fish group samples were analysed per depth.

¹³C/¹²C and ¹⁵N/¹⁴N ratios in the samples were determined using continuous-flow isotope mass spectroscopy (CF-IRMS) (Preston & Owens 1983). Weighed samples of material (1 mg) were oxidized and the N₂ and CO₂ passed to a single inlet dual collector mass spectrometer (PDZ Europa ANCA SL 20–20 system). Isotope ratios were expressed as parts per thousand (‰) differences from a standard reference material:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$$

where δ = the measure of heavy to light isotope in the sample, X = ¹³C or ¹⁵N and R = the corresponding ratio (¹³C/¹²C or ¹⁵N/¹⁴N).

International Standard references are Vienna Pee Dee Belemnite (vPDB) for carbon, and atmospheric N₂ for nitrogen. However, to calibrate the system and compensate measurement drift with time, cornflour and cod (*Gadus morhua* L.) white muscle, with known signatures, were used as internal reference materials when analysing water samples and animal material, respectively. Experimental precision, based on the standard deviations of the internal reference replicates, was 0.12‰ for δ¹³C and 0.13‰ for δ¹⁵N.

DATA ANALYSIS

To assess main modifications in POM sources' isotopic signatures during the year, average δ¹³C and δ¹⁵N values of Rhone River POM and marine phytoplankton (offshore seawater POM) were determined for both periods of high (winter, spring) and low (summer) river discharge. Student's *t*-tests were performed independently on the calculated δ¹³C and δ¹⁵N to test within-year signature changes by source, and among-sources signature differences for each period.

In aquatic systems, δ¹³C and δ¹⁵N generally increase by 1–2‰ and 2.5–4.5‰ from food to consumer, respectively (De Niro & Epstein 1978; Minagawa & Wada 1984; Wada *et al.* 1991; Post 2002). These values were used to assess food web structure off the Rhone River. The comparison of flatfish and benthic prey isotopic signatures with the δ¹³C and δ¹⁵N values obtained for Rhone River POM and marine phytoplankton allowed the description of benthic food webs at each depth (δ¹³C vs. δ¹⁵N graphs) and estimation of the average (mean ± SD) trophic increases in isotopic signatures for the whole study area (for detail, see Darnaude 2003). On average, δ¹³C increased by 1.80 ± 0.21‰ from prey to predator off the Rhone River, while the mean trophic increases in δ¹⁵N were 2.60 ± 0.05‰ and 3.20 ± 0.10‰ for herbivores and carnivores, respectively.

Intra- and interspecific differences in fish isotopic signature were tested by two-way (species × life stage) ANOVAs performed separately on δ¹³C and δ¹⁵N values. One-way (depth range) ANOVAs were also performed to test depth-related δ¹³C variations in the juveniles and adults of *C. linguatula* and in the adults of *A. laterna*, *B. luteum* and *S. solea*. In each case, data

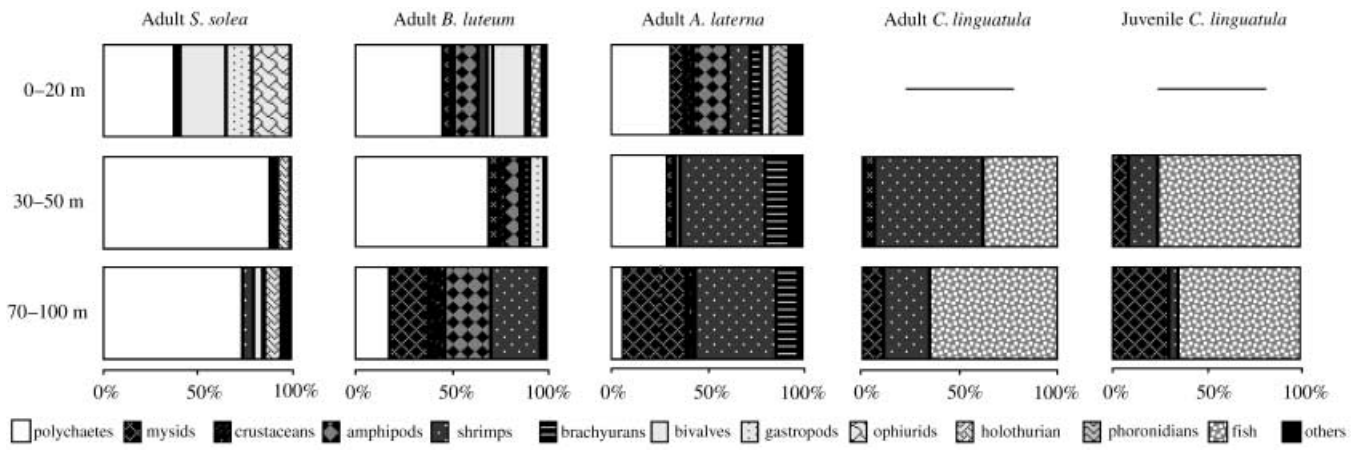


Fig. 1. Depth variation in diet (expressed as dry weight percentage of prey in stomach contents) in the juveniles and adults of *Citharus linguatula* and in the adults of *Arnoglossus laterna*, *Buglossidium luteum* and *Solea solea*.

were log-transformed to stabilize variance, and *post-hoc* comparisons of means were performed using Student–Newman–Keuls tests. Only differences in isotopic signatures associated with $P < 0.05$ were considered to be statistically significant. Because significant differences in carbon signatures in fish can arise not only from differences in food sources (terrestrial vs. marine) but also from differences in trophic levels ($\delta^{15}\text{N}$), differences in $\delta^{13}\text{C}$ do not allow the assessment of the extent of terrestrial-POM uptake by the fish. To solve this problem, fish trophic levels (TL) in the case of an exclusively marine POM-based diet were calculated using the equation:

$$\text{TL} = [(\delta^{15}\text{N}_{\text{fish}} - (\delta^{15}\text{N}_{\text{phytoplankton}} + 2.6))/3.2] + 2$$

where 2.6 and 3.2 = average trophic increases in $\delta^{15}\text{N}$ (‰) found in the study area for herbivores and carnivores, respectively.

They were then used to obtain corresponding theoretical marine carbon signatures ($\delta^{13}\text{C}_{\text{th}}$) for all fish groups by using the equation:

$$\delta^{13}\text{C}_{\text{th}} = \delta^{13}\text{C}_{\text{phytoplankton}} + [(TL - 1) \times 1.8]$$

where 1.8 = average trophic increase in $\delta^{13}\text{C}$ (‰) observed in the benthic communities of the study area.

The comparison of fish theoretical and observed $\delta^{13}\text{C}$ values allowed estimating the extent of their terrestrial POM uptake off the Rhone River.

Results

FISH LIFE-STRATEGIES

Different depth distributions were observed between the five species, reflecting differences in habitat-use. Depth distribution changed with age in *A. laterna*, *B. luteum* and *S. solea*. In these three species, most juveniles (> 98%) occurred at 0–20 m depth. Adults occurred at all depth ranges, but most of them (55% in *A. laterna*, 62% in

B. luteum and 47% in *S. solea*) were found at 30–50 m. In *S. lascaris* and *C. linguatula*, juveniles and adults had similar distributions. However, *S. lascaris* was taken only on nearshore sandy bottoms (0–20 m depth), whereas *C. linguatula* occurred only offshore, on the muddy bottoms of 30–100 m in depth.

The five species showed important differences in food preferences and diet adaptability (Table 1, Fig. 1) despite occupying the same habitats. *Buglossidium luteum* had the last specialized diet, with similar proportions of polychaetes, molluscs (mainly bivalves) and crustaceans. *Solea solea*, *S. lascaris* and *A. laterna* also preyed on a wide variety of benthic organisms but showed clear preferences for polychaetes, bivalves and crustaceans, respectively. In *C. linguatula* the diet was highly specialized, consisting almost exclusively of fish and crustaceans (mysids and shrimps).

In all cases, ontogenetic changes in diet were observed; however, the extent of differences between juvenile and adult fish varied according to species (Table 1). Ontogenetic changes in diet were clearest in *B. luteum* and *S. lascaris*. In *B. luteum*, juvenile diet was dominated by crustaceans (cumaceans, amphipods and copepods) and adult diet by polychaetes (deposit feeders and carnivores). In *S. lascaris*, juveniles ate mainly polychaetes (suspension feeders), whereas adults fed essentially on bivalves (siphons). In the three other species, the main prey categories remained the same for both life stages, but with some modifications in the size and nature of the prey ingested. In *A. laterna*, both life stages consumed mainly crustaceans (W% > 68%). However, juvenile *A. laterna* fed mainly on cumaceans and amphipods, while the adults consumed mainly shrimps, brachyurans and mysids. In *S. solea*, polychaetes dominated the diet of both juveniles and adults (W% > 34%) but, as the fish matured, subsurface deposit-feeding and carnivorous polychaetes progressively replaced surface deposit-feeding polychaetes in the diet. In *C. linguatula*, fish were the main prey item irrespective of the age (W% > 64%), but prey size increased with growth, and shrimps were progressively replaced by mysids.

Table 1. Global diet (expressed as dry weight percentage of prey in stomach contents) obtained for the juveniles (Juv.) and adults (Ad.) of *Arnoglossus laterna*, *Buglossidium luteum*, *Citharus linguatula*, *Solea lascaris* and *S. solea* off the Rhone River. N = sample size; +, values less than 0.01%; –, prey category not found

	<i>A. laterna</i>		<i>B. luteum</i>		<i>C. linguatula</i>		<i>S. lascaris</i>		<i>S. solea</i>	
	Juv.	Ad.	Juv.	Ad.	Juv.	Ad.	Juv.	Ad.	Juv.	Ad.
N	58	596	32	92	31	51	47	32	33	97
Size range (total length, cm)	20–49	81–132	32–48	83–126	63–91	161–237	49–96	160–212	32–92	264–374
Depth range of life (in m)	0–20	0–100	0–20	0–100	30–100	30–100	0–20	0–20	0–20	0–100
Polychaetes	21.5	26.0	21.9	56.8	–	1.1	65.6	2.9	34.5	75.9
Surface deposit feeders	2.1	4.7	–	+	–	–	6.6	0.4	24.4	3.0
Subsurface deposit feeders	+	0.3	–	17.9	–	0.6	–	–	10	54.1
Suspension feeders	11.5	13.5	–	0.9	–	–	59.0	1.7	–	5.5
Carnivores	7.9	7.5	21.9	38.0	–	0.5	–	0.8	+	13.3
Sipunculids	–	–	–	–	–	–	–	–	–	2.2
Crustaceans	71.3	68.3	51.2	27.4	35.2	25.3	26.6	15.6	34.2	5.3
Copepods	4.5	0.2	16.4	1.2	–	–	–	0.9	–	–
Leptostraceans	3.4	–	–	–	–	–	–	–	–	–
Mysids										
< 5 mm	–	–	–	4.2	29.8	2.2	6.5	3.0	5.5	–
5–10 mm	–	10.4	–	–	–	7.0	–	5.3	–	–
Cumaceans	47.5	0.6	17.4	1.3	–	–	13.7	2.2	–	–
Amphipods	15.9	5.7	17.4	8.3	–	–	6.4	4.2	17.7	–
Shrimps										
Alpheidae	–	–	–	–	–	0.2	–	–	–	1.1
Crangonidae										
< 20 mm	–	33.0	–	9.8	5.4	–	–	–	–	0.1
20–40 mm	–	6.1	–	–	–	15.9	–	–	11.0	2.2
Pagurids	–	0.9	–	–	–	–	–	–	–	0.6
Brachyurans	–	11.4	–	2.4	–	–	–	–	–	1.3
Molluscs	7.2	1.7	26.8	15.6	–	+	7.8	79.7	26.6	7.8
Bivalves										
Juveniles < 10 mm	7.2	–	10.4	–	–	+	1.0	–	6.0	+
Siphons	–	1.7	–	14.8	–	–	6.8	78.4	20.6	5.4
Gastropods	–	+	16.4	0.8	–	–	–	1.3	–	2.4
Echinoderms	–	+	+	+	–	–	–	1.8	1.5	8.7
Ophiurids	–	+	+	+	–	–	–	1.8	1.5	3.0
Holothurians	–	–	–	–	–	–	–	–	–	5.7
Phoronidians	–	3.8	–	+	–	–	–	–	3.2	–
Fish (Gobiids)	–	0.2	+	+	64.8	73.5	–	–	–	0.1
< 30 mm	–	+	+	+	64.8	1.1	–	–	–	–
30–50 mm	–	0.2	–	–	–	72.4	–	+	–	0.1

Diet varied with depth, especially in adult *A. laterna*, *B. luteum* and *S. solea* (Fig. 1). In these three fish groups, mollusc and crustacean consumptions were maximal at 0–20 m and at 70–100 m, respectively, and a common peak in polychaete ingestion was observed at 30–50 m for *B. luteum* and *S. solea*. In *C. linguatula*, main preys were always fish, shrimps and mysids, but their respective contributions to the diet varied with depth and the adults ate polychaetes only at 30–50 m depth.

FISH ISOTOPIC SIGNATURES

Nitrogen and carbon isotopic signatures differed significantly between species ($P < 0.001$) and life stage ($P < 0.01$), which suggested intra- and interspecific differences in trophic levels and food origin (Table 2). In all species, $\delta^{15}\text{N}$ increased significantly ($P < 0.01$) between juveniles and adults, suggesting increased trophic level with growth.

However, the level of increase varied among species, with a minimum ($< 1.0\text{‰}$) in the two sole species and a maximum ($> 2.6\text{‰}$) in *C. linguatula*. Consequently, interspecific differences in nitrogen signature varied by life stage. Among juveniles, $\delta^{15}\text{N}$ was significantly lower ($< 9\text{‰}$) in *A. laterna*, *B. luteum* and *C. linguatula* than in *S. solea* and *S. lascaris* ($> 10\text{‰}$). Among adults, *A. laterna* ($\delta^{15}\text{N} = 10.1\text{‰}$) and *C. linguatula* ($\delta^{15}\text{N} = 11.6\text{‰}$) had significantly lower and significantly higher nitrogen signatures, respectively, than the other species. Carbon isotopic signature was similar for juveniles and adults in *A. laterna*, *C. linguatula* and *S. solea*, but differed significantly ($P < 0.05$) between juveniles and adults in *B. luteum* and *S. lascaris* (Table 3). $\delta^{13}\text{C}$ was significantly lower in juvenile *S. solea* (-20.0‰), and higher in juvenile *C. linguatula* and *B. luteum* ($> -17.6\text{‰}$) than in *A. laterna* and *S. lascaris*. For adults, carbon signature differed significantly between all species. Adult *S. solea* had the

Table 2. Carbon and nitrogen isotopic signatures (mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N} \pm \text{SE}$, in‰) in the five flatfish studied off the Rhone River. –, fish group absent within depth range

	0–20 m depth		30–50 m depth		70–100 m depth		global: 0–100 m	
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<i>A. laterna</i>								
Juveniles	-18.93 ± 0.46	8.52 ± 0.16	-18.93 ± 0.46	8.52 ± 0.16	–	–	-18.93 ± 0.46	8.52 ± 0.16
Adults	-16.75 ± 0.25	10.49 ± 0.47	-18.23 ± 0.26	10.10 ± 0.14	-18.25 ± 0.25	9.69 ± 0.62	-18.23 ± 0.26	10.10 ± 0.14
<i>B. luteum</i>								
Juveniles	-17.52 ± 0.15	8.77 ± 0.18	-17.52 ± 0.15	8.77 ± 0.18	–	–	-17.52 ± 0.15	8.77 ± 0.18
Adults	-18.47 ± 0.31	11.18 ± 0.21	-19.04 ± 0.22	11.07 ± 0.09	-17.99 ± 0.52	10.97 ± 0.31	-19.04 ± 0.22	11.07 ± 0.09
<i>C. linguatula</i>								
Juveniles	–	–	-17.60 ± 0.08	8.98 ± 0.08	-17.58 ± 0.09	8.85 ± 0.08	-17.60 ± 0.08	8.98 ± 0.08
Adults	–	–	-17.64 ± 0.08	11.63 ± 0.11	-17.67 ± 0.10	11.67 ± 0.10	-17.64 ± 0.08	11.63 ± 0.11
<i>S. lascaris</i>								
Juveniles	-18.71 ± 0.15	10.69 ± 0.12	-18.71 ± 0.15	10.69 ± 0.12	–	–	18.71 ± 0.15	-10.69 ± 0.12
Adults	-16.96 ± 0.22	11.10 ± 0.17	-16.96 ± 0.22	11.10 ± 0.17	–	–	-16.96 ± 0.22	11.10 ± 0.17
<i>S. solea</i>								
Juveniles	-20.03 ± 0.33	10.07 ± 0.14	20.03 ± 0.33	10.07 ± 0.14	–	–	-20.03 ± 0.33	10.07 ± 0.14
Adults	-19.07 ± 0.23	11.00 ± 0.13	-20.14 ± 0.38	11.06 ± 0.15	-20.06 ± 0.38	11.05 ± 0.23	-20.14 ± 0.38	11.06 ± 0.15

Table 3. Temporal variation in isotopic signature observed for the Rhone River particulate organic matter (POM) and marine phytoplankton (offshore seawater POM); N = sample size; t -test = results of Student's tests realized on isotopic signatures in each case. Probabilities (P) inferior to 0.05 indicate significant within-year signature changes by source or among-sources signature differences for each period

	Period of high river discharge (winter–spring)	Period of low river discharge (summer)	t -test
	$N = 6$	$N = 3$	
$\delta^{13}\text{C}$ (mean \pm SE)			
Rhone River POM (terrestrial)	-25.52 ± 0.24	-26.62 ± 0.12	$P < 0.001$
Offshore seawater POM (marine)	-22.03 ± 0.22	-23.01 ± 0.37	$P < 0.001$
t -test	$P < 0.001$	$P < 0.001$	
$\delta^{15}\text{N}$ (mean \pm SE)			
Rhone River POM (terrestrial)	4.12 ± 0.10	2.82 ± 0.16	$P < 0.001$
Offshore seawater POM (marine)	2.41 ± 0.09	2.25 ± 0.11	$P < 0.01$
t -test	$P < 0.001$	$P < 0.01$	

lowest (-20.1‰) and *S. lascaris* the highest (-17.0‰) $\delta^{13}\text{C}$. Carbon signature was similar at 30–50 m and 70–100 m in both juvenile and adult *C. linguatula* ($P > 0.07$). However, significant differences in carbon signature were observed with depth in the adults of *A. laterna*, *B. luteum* and *S. solea* ($P < 0.001$), the lowest $\delta^{13}\text{C}$ values occurring at 30–50 m.

TERRESTRIAL POM UPTAKE

Carbon and nitrogen signatures varied significantly during the year for both POM sources (Table 3). However, carbon signature was always significantly lower ($> 3.5\text{‰}$) for Rhone River POM (annual mean $\delta^{13}\text{C} = -26.11 \pm 0.23\text{‰}$) than for marine phytoplankton (annual mean $\delta^{13}\text{C} = -22.36 \pm 0.23\text{‰}$). This allowed the transfers of these two POM sources to be traced within food webs and the extent of terrestrial POM uptake by the fish to be determined.

Isotopic signatures indicated the incorporation of material of terrestrial origin in the flesh of all fish species, at least during one benthic life stage (Fig. 2). $\delta^{13}\text{C}$ was only slightly lower than would be expected in an exclusively marine diet for adult *C. linguatula* and for juvenile and adult *A. laterna*, but was particularly low in juvenile *S. lascaris*, adult *B. luteum*, and juvenile and adult *S. solea*.

Bathymetric differences in diet and terrestrial POM use by the benthos explained most of the differences in isotopic signature observed among fish groups. At 0–20 m, terrestrial POM exploitation by benthic prey was reduced, and only deposit-feeding and carnivorous polychaetes exploited mainly terrestrial POM for their growth (Fig. 3). The juveniles and adults of *A. laterna*, the juveniles of *B. luteum* and the adults of *S. lascaris* (mainly bivalve and crustacean feeders, Table 2, Fig. 1) were located at the top of the marine phytoplankton-based food web. *Solea solea* juveniles, which ingested

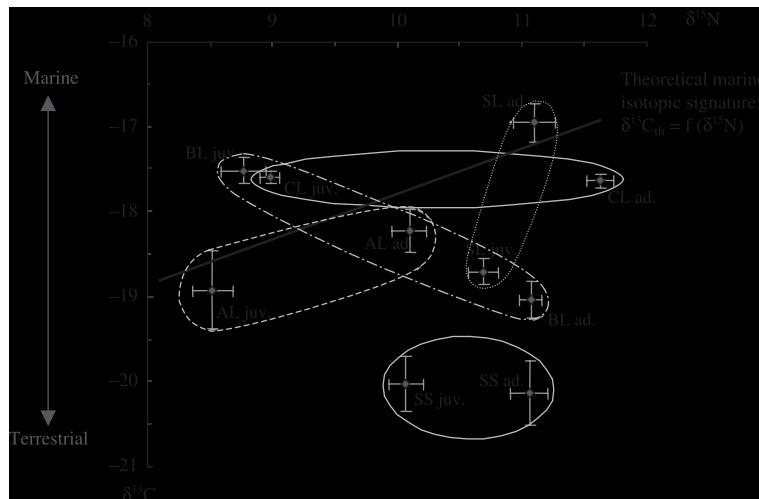


Fig. 2. Terrestrial vs. marine POM use during juvenile (*juv.*) and adult (*ad.*) growth in *Arnoglossus laterna* (*AL*), *Buglossidium luteum* (*BL*), *Citharus linguatula* (*CL*), *Solea lascaris* (*SL*) and *Solea solea* (*SS*). Comparison of obtained (mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N} \pm \text{SE}$ in ‰) and theoretical (dark line in bold) isotopic signature allowed estimation of the degree of terrestrial material uptake by the fish (for details see Materials and methods).

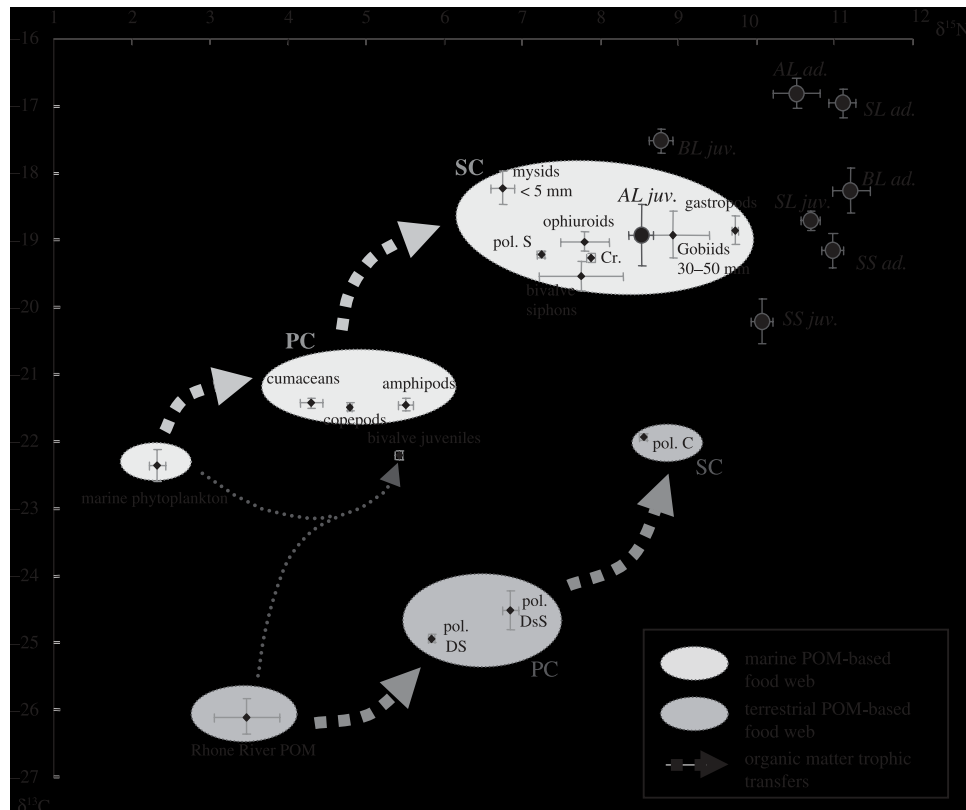


Fig. 3. Plot of $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ (mean‰ \pm SE) obtained for the benthic food web components of the juveniles (*juv.*) and adults (*ad.*) of *Arnoglossus laterna* (*AL*), *Buglossidium luteum* (*BL*), *Solea lascaris* (*SL*) and *Solea solea* (*SS*) at 0–20 m depth. *Cr.*, Crangonidae (20–40 mm), *PC* primary consumers, *POM* particulate organic matter, *pol.* polychaetes (*C* carnivorous, *DS* surface deposit feeding, *DsS* subsurface deposit feeding, *S* suspension feeding), *SC* secondary consumers. Detailed isotopic signatures (means \pm SD) of benthic prey can be found in Darnaude *et al.* (2004b).

significant amounts ($W\% > 34\%$) of deposit feeding polychaetes, had a very different position on the graph, denoting a substantial dependency on terrestrial POM source for their growth. Adult *S. solea* and *B. luteum* and juvenile *S. lascaris* (deposit feeding or carnivorous-polychaete feeders) had intermediate positions, indicating

reliance on marine primary production, but with a partial exploitation of terrestrial POM.

At 30–50 m depth, terrestrial POM was exploited by bivalve juveniles, brachyurans and Crangonidae shrimps, and all polychaetes exploited mainly river-borne material for growth (Fig. 4). The low contribution of polychaetes

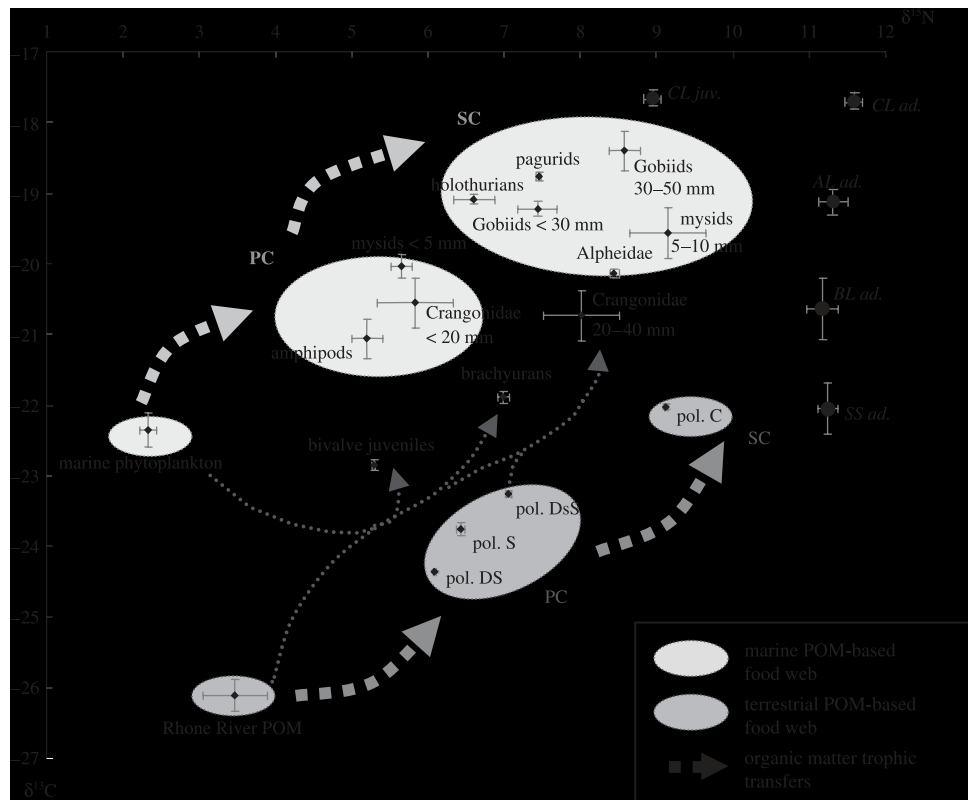


Fig. 4. Plot of $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ (mean‰ \pm SE) obtained for the benthic food web components of the juveniles (*juv.*) and adults (*ad.*) of *Citharus linguatula* (*CL*) and the adults of *Arnoglossus laterna* (*AL*), *Buglossidium luteum* (*BL*) and *Solea solea* (*SS*) at 30–50 m depth. *PC* primary consumers, *POM* particulate organic matter, *pol.* polychaetes (*C* carnivorous, *DS* surface deposit feeding, *DsS* subsurface deposit feeding, *S* suspension feeding), *SC* secondary consumers. Detailed isotopic signatures (means \pm SD) of benthic prey can be found in Darnaude *et al.* (2004b).

to the diet of *C. linguatula* ($W\% < 2\%$) (Fig. 1) was responsible for its position at the top of the marine POM-based food web. However, the consumption of Crangonidae and the occasional ingestion of polychaetes by adult *C. linguatula* at this depth resulted in a slightly lower $\delta^{13}\text{C}$ than would be expected in an exclusively marine diet (Fig. 2). Prey isotopic signatures fully explained the differences in carbon signature observed for the adults of *S. solea*, *B. luteum* and *A. laterna*. Increased consumption of polychaetes ($W\%$) resulted in decreased $\delta^{13}\text{C}$ (Fig. 1). Adult *S. solea* (polychaetes $W\% > 88\%$) were at the top of the terrestrial POM-based food web, while adult *A. laterna* (polychaetes $W\% < 25\%$) occurred near the top of the marine phytoplankton-based web. Adult *B. luteum* (polychaetes $W\% = 70\%$) were intermediate in both webs.

At 70–100 m depth, benthic organisms showed little exploitation of river POM, and only subsurface deposit feeding polychaetes depended on terrestrial material for growth (Fig. 5). Their absence in the diet of *C. linguatula* juveniles and adults and their very low contribution to the diet of adult *A. laterna* and *B. luteum* ($W\% < 1\%$) (Fig. 1) explained why these fish were positioned at the top of the marine POM-based food web. Conversely, adult *S. solea*, that ingested substantial amounts of subsurface deposit feeding polychaetes ($W\% > 29\%$), were positioned between the marine and the terrestrial POM-based food webs.

Thus, terrestrial POM uptake was least in *C. linguatula*, whose diet always included very few prey able to exploit terrestrial material for growth. It was greatest in *S. solea*, where deposit feeding polychaete ingestion by juveniles and adults was high and where adults were found mainly at 30–50 m depth. In *B. luteum*, *A. laterna* and *S. lascaris*, main terrestrial POM uptake was intermediate. It occurred in the life stage showing the highest polychaete ingestion and/or present at 30–50 m depth.

Discussion

Reliable isotopic studies of terrestrial organic matter transfer within coastal food webs, i.e. based on the simultaneous analysis of at least two elements, are rare (Camusso *et al.* 1999; Melville & Connolly 2003). Few include benthic top predators such as flatfish (Deegan & Garritt 1997; Kwak & Zedler 1997; Paterson & Whitfield 1997), and fewer still suggest a significant influence of river-borne material on fish populations (Lee 2000; Sheaves & Molony 2000). The present study demonstrated the importance of terrestrial carbon use by juvenile and adult bottom-dwelling fish, even in periods of moderate river discharge. This was detected only as a result of the comprehensive reconstruction of fish benthic food webs at different depths, which was facilitated by the presence of only two main POM supplies (river POM and marine phytoplankton) in

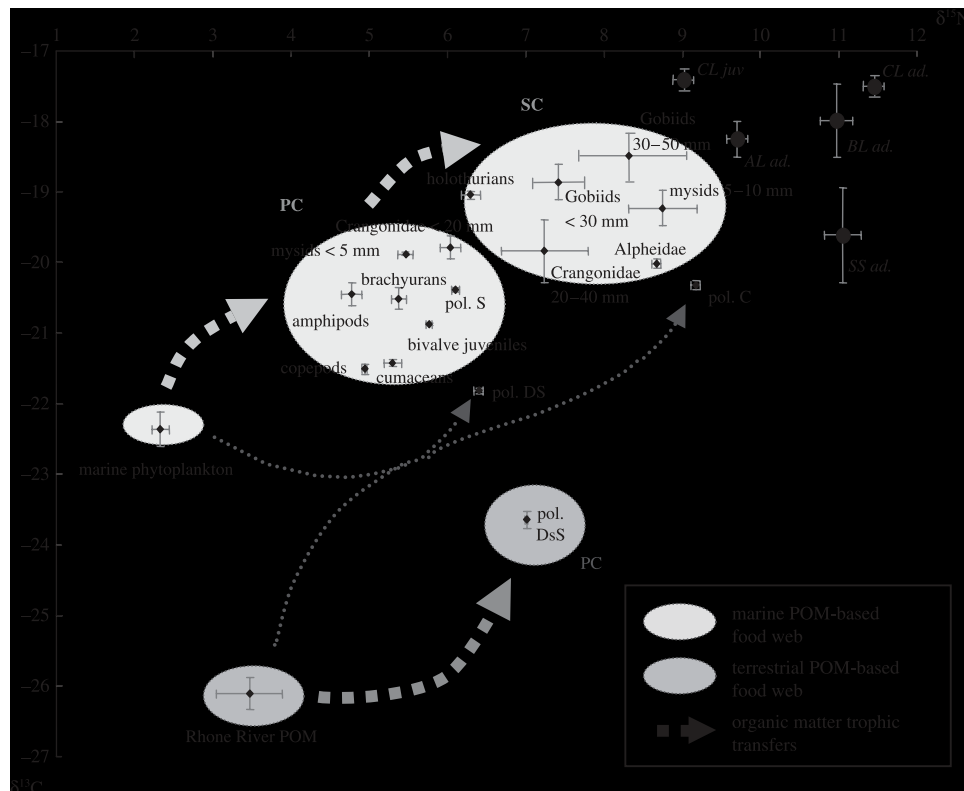


Fig. 5. Plot of $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ (mean‰ \pm SE) obtained for the benthic food web components of the juveniles (*juv.*) and adults (*ad.*) of *Citharus linguatula* (*CL*) and the adults of *Arnoglossus laterna* (*AL*), *Buglossidium luteum* (*BL*) and *Solea solea* (*SS*) at 70–100 m depth. *PC* primary consumers, *POM* particulate organic matter, *pol.* polychaetes (*C* carnivorous, *DS* surface deposit feeding, *DsS* subsurface deposit feeding, *S* suspension feeding), *SC* secondary consumers. Detailed isotopic signatures (means \pm SD) of benthic prey can be found in Darnaude *et al.* (2004b).

the study area (Darnaude *et al.* 2004a). The number of potential POM sources for the benthos is usually higher in estuarine ecosystems (Riera 1998; Lee 2000). Therefore, it is possible that a non-negligible uptake of terrestrial POM by marine benthic fish also occurs in other studied areas (e.g. Deegan & Garrit 1997; Kwack & Zedler 1997) where system complexity prevents its detection by stable isotope methods.

FISH ECOLOGY AND SENSITIVITY TO RIVER FLOODS

Because of the interspecific and depth differences in terrestrial POM use by the benthos observed off the Rhone River (Darnaude *et al.* 2004b), flatfish depth distribution and diet can play a key role in determining their sensitivity to Rhone River floods. Flooding events have been shown to result not only in an increase in benthic prey densities, but also in modifications of benthic community compositions, mainly in favour of deposit feeding and carnivorous polychaetes (Salen-Picard *et al.* 1997; Massé 2000). These effects should be the greatest at 30–50 m depth, where most of the terrestrial POM is deposited (Bouloubassi *et al.* 1997; Darnaude *et al.* 2004b).

Juvenile flatfish habitat usually corresponds to the coastal margins of the adult habitat, which reduces intraspecific competition and favours juvenile growth

(Gibson 1994). However, not all flatfish follow this general pattern. Some species display similar depth distributions throughout their benthic lives (Marinero & Bouabib 1983; Garcia-Rodriguez & Eesteban 2000; Bolle, Rijnsdorp & Van der Veer 2001). Among the five species studied, both strategies were observed. In *S. lascaris* and *C. linguatula*, juveniles and adults were found within the same depth ranges. By contrast, *S. solea*, *B. luteum* and *A. laterna* juveniles occurred at 0–20 m whereas adults were found from 10 to 100 m depth. As terrestrial POM uptake by the benthos peaks at 30–50 m, the shallow distribution of *S. solea*, *B. luteum* and *A. laterna* juveniles and of all life stages of *S. lascaris* prevent their benefiting from the greatest river input-linked increases in prey density, unlike adult *S. solea*, *B. luteum* and *A. laterna* and all the life stages of *C. linguatula*.

Fish diet composition depends mainly on prey detection mode and gut morphology (De Groot 1971). Soleidae are morphologically adapted to the ingestion of vulnerable prey with low mobility, such as polychaetes or bivalves. Conversely, Bothidae and Citharidae are visual hunters capable of capturing and ingesting larger and more mobile prey, such as crustaceans and fish. This explains the dominance of polychaetes and bivalves in the diets of *S. solea*, *B. luteum* and *S. lascaris* and the predominance of crustaceans and fish in the diets of *A. laterna* and *C. linguatula*. Modification of diet with growth is mainly due to differences in metabolic needs

between juveniles (small size, energy allocated to growth) and adults (larger size, energy allocated to growth and reproduction) (Nikolskii 1969; Gerking 1994). However, in flatfish it also reflects the progressive adaptation to benthic life (Sorbe 1981). In general, the ingestion of small crustaceans (copepods, cumaceans) decreases with growth, and food progressively diversifies until large benthic invertebrates are taken by the adults (Rogers & Jinadasa 1989). Our results confirm this pattern, but ontogenetic changes in diet varied between species. In *C. linguatula*, prey size increased without a pronounced modification in diet composition. In the four other species, however, ontogenetic changes in diet involved not only a shift in prey size, but also a modification of the taxa ingested. As deposit feeding and carnivorous polychaetes are the only benthic invertebrates to principally exploit terrestrial POM, consumers of these species, such as adult *S. solea* and *B. luteum*, would benefit most from increased river POM inputs. All life stages of *S. lascaris* and adult *A. laterna* may also benefit from river floods, as an increase in terrestrial POM availability may result in a significant increase in the density of suspension feeding polychaetes, bivalves and Crangonidae shrimps. Conversely, Rhone River floods would have little impact on juvenile and adult *C. linguatula*, whose prey do not substantially exploit terrestrial POM.

Regarding feeding adaptability, the five species showed very different strategies. *Citharus linguatula* had a very specialized diet and a low trophic adaptability, as confirmed by the constancy of its diet irrespective of depth-range. By contrast, *S. solea*, *B. luteum*, *A. laterna* and *S. lascaris* consumed a wide range of prey items, and seemed able to adapt their diet according to prey availability in their immediate environment. They ingested highest amounts of bivalves at 0–20 m, polychaetes at 30–50 m and crustaceans at 70–100 m, the depths at which these prey items were the most abundant (Darnaude *et al.* 2004b). Such ‘opportunistic’ feeding behaviour should allow all life stages of *S. solea*, *S. lascaris*, *B. luteum* and *A. laterna* to exploit the selective increases in benthic prey abundances linked to terrestrial POM inputs, notably during periods of high river discharge.

As predator size determines the size-range of prey in the diet (Cohen *et al.* 1993), fish trophic level usually increases with size, a pattern observed in all five species studied. Trophic levels varied from 3.1 to 3.7 in juveniles and 3.5–4.0 in adults. The increase in trophic level with growth was low in the two sole species, due to an adult diet composed mainly of primary consumers (deposit feeding polychaetes or bivalves). Therefore, despite their different sizes, the adults of *B. luteum*, *S. solea* and *S. lascaris* showed similar trophic levels (around 3.8). This has important implications with regard to the intensity of terrestrial POM transfer to fish. Due to energy loss within trophic pyramids, biomass decreases inversely proportional to animal position in the food web (Pimm 1982). Therefore, the consumption of primary consumers that directly exploit terrestrial

POM for growth (deposit-feeding polychaetes, bivalves) would be more advantageous for fish than the ingestion of secondary consumers that rely on it (carnivorous polychaetes, brachyurans, shrimps). According to the trophic levels observed in the five species, adult *S. solea*, *B. luteum* and *S. lascaris* should be favoured more by increased terrestrial POM use by their prey, than adult *A. laterna* or *C. linguatula*.

IMPLICATIONS FOR FISH PRODUCTION

Terrestrial POM constitutes only a fraction of Rhone River inputs to the sea. The river’s high dissolved organic matter and nutrient inputs influence primary production intensity over the entire NW Mediterranean basin (Tusseau-Vuillemain 1998), thereby determining food quantity and quality for larval fish. However, unlike particulate inputs, dissolved inputs are relatively constant from year to year (Cauwet 1996) and local annual primary production is largely independent of river discharge (Lefèvre *et al.* 1997). River floods should therefore have little impact on fish larval life.

The potential impacts of river floods on fish population dynamics and their consequences for local fisheries would therefore depend on the benthic life stage(s) affected by terrestrial POM uptake. In fish, year-class strength is thought to be determined mainly in the late larval and early juvenile stages, where most mortality occurs (Cushing 1982). As changes in natural mortality could lead to large differences in cohort size (Leggett & DeBlois 1994; Bailey *et al.* 1995), factors that favour survival at the juvenile stages can strongly influence population dynamics. In flatfish, food quality and quantity have stronger impacts on juvenile growth and survival than density-dependent regulation, temperature and sediment type (Fonds *et al.* 1992; Rogers 1992; Van der Veer & Witte 1993; Rogers 1994). Increased juvenile prey abundance should therefore highly favour growth and survival, increasing the number of fish recruiting to the adult stock. In this case, increased fish catches would be expected in the years directly following a flooding event, with a species-dependent response time lag reflecting age at recruitment to the fishery. This has already been shown for *S. solea* (Salen-Picard *et al.* 2002; Darnaude *et al.* 2004a). Observations of juvenile diet from the present study suggest a similar response in *S. lascaris*, *A. laterna* and *B. luteum*.

Interannual variation in reproductive success can also have an important influence on fish population dynamics, as it controls benthic recruitment through the amount of eggs released in the environment (Miller 1994). Feeding influences both size at first maturity (Morgan 2004) and adult growth and condition (Bromley, Ravier & Witthames 2000). Fecundity increases with size in fish (Horwood 1993) and female condition influences egg quantity (Horwood, Greer Walker & Witthames 1989) and quality (Rijnsdorp *et al.* 1991). As older and larger females show higher fecundity and produce more recruits with high survival rates (Cardinale & Arrhenius 2000), the condition

and growth of spawning fish, which is linked closely to their food supply, can have an impact on future year-class strength in fish. Therefore, terrestrial POM uptake by adult fish after a flood would further optimize species reproductive success for several years, resulting in a long-term increase in fish catches, with a time lag depending on spawning frequency and age at recruitment to the fishery. This phenomenon, already demonstrated for the common sole *S. solea* (Salen-Picard *et al.* 2002; Darnaude *et al.* 2004a), should also occur in *B. luteum* and, to a lesser extent, *A. laterna* and *S. lascaris*.

Thus, dependent on fish depth distribution, food preference, dietary adaptability, trophic level and terrestrial POM uptake in moderate river discharge conditions, Rhone river floods can be predicted to have little impact on *C. linguatula* populations but would increase the four other species' local stocks for several years, with a maximum impact on *S. solea*.

Conclusion

While the present study suggests that river floods will enhance fishery production of most of the species studied for several years, further studies linking time variation in river discharge, prey abundance, fish fecundity and fish recruitment are still required before the exact nature of the flatfish response can be predicted accurately. However, the use of carbon and nitrogen stable isotopes allowed the detection and description of terrestrial carbon incorporation into five marine flatfish off the Rhone River delta in conditions of moderate river discharge. Interspecific differences in fish diet and habitat-use fully explained the intensity of terrestrial POM uptake during benthic life. As fish ecology will determine a species ability to exploit or not the increases in benthic prey production linked to terrestrial POM inputs, fish ecology controls species' sensitivity to modifications in river discharge and must be assessed carefully before estimating the impacts of river floods for coastal fisheries production. Such impacts should be maximal in large polychaete feeders with low trophic level, high trophic adaptability and wide bathymetric distribution, such as *Solea solea*.

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