

Influence of trawl type on the composition and diversity of deep benthopelagic fish and decapod assemblages off the Catalan coasts (western Mediterranean)

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SUMMARY: A series of 57 (600-750 m) and 32 (1184-1320 m) hauls were compiled to compare data from four trawl types in analyses of the species composition and diversity of deep benthopelagic fish and decapods off the Catalanian coasts (western Mediterranean). Two 1-warp trawls (OTSB-14 and MTS-25) and two 2-warp trawls (a commercial trawl [CT] and a GOC73) were used, from hauls performed between 1988 and 2007 were compiled. At 600-750 m the OTSB-14 hauls were separated in multi-dimensional scaling (MDS) from hauls performed with MTS-25, CT, and GOC73. Ordination of hauls along DIM1 of MDS was significantly correlated (Spearman's r) with mesh size at codend, bridle length, and vertical opening of trawls. When CT and GOC73 were compared with MTS-25, the most dissimilar species were *Aristeus antennatus*, *Galeus melastomus* and *Trachyrhynchus scabrus*. A particular case was *A. antennatus*, with a significantly higher abundance in MTS-25 catches than the rest of the trawls. At 1200-1300 m the OTSB-14 and MTS-25 hauls were segregated in MDS analysis. DIM2 was correlated with the sampling period (month), indicating a temporal effect on haul composition. At 1200-1300 m the main dissimilarities between OTSB-14 and MTS-25 were marked by *Alepocephalus rostratus* and *A. antennatus* (caught with MTS-25), and by *Cataetyx alleni*, the Notacanthidae *Notacanthus bonapartei* and *Polyacanthonotus rissoanus*, and *Plesionika acanthonotus* (caught with OTSB-14). As a conclusion, OTSB-14 showed a significantly higher abundance in catches than MTS-25, CT and GOC73, and a higher S (number of species) and J (equitability) than MTS-25. On the lower slope seasonality influenced trawl comparisons; however, it is likely that MTS-25, with higher vertical height than OTSB-14, caught the benthopelagic fish *A. rostratus* more efficiently, explaining the higher biomass from MTS-25 there. MTS-25 positively selected *A. antennatus*, in parallel to a negative catchability for other species.

Keywords: deep sea, trawl comparison, diversity, decapod crustaceans, fishes, *Aristeus antennatus*, OTSB.

RESUMEN: INFLUENCIA DEL TIPO DE ARTE DE ARRATRE UTILIZADO EN LA COMPOSICIÓN Y LA DIVERSIDAD DE LAS COMUNIDADES DE PECES Y CRUSTÁCEOS DECÁPODOS BENTOPELÁGICOS DE LA COSTA CATALANA (MEDITERRÁNEO OCCIDENTAL). – Se recopilieron datos sobre la abundancia de peces y crustáceos decápodos de un total de 57 (600-750 m) y 32 (1184-1320 m) lances de una zona concreta de las costas de Cataluña (Mediterráneo Occidental) para comparar la composición y diversidad de estas comunidades en función de la utilización de cuatro tipos distintos de artes de arrastre bentónicos. Dos tipos de arte de arrastre de 1 cable (OTSB-14 y MTS-25) y dos más de 2 cables (un arte comercial, CT y un GOC73) fueron utilizados en lances efectuados entre 1988 y 2007. A 600-750 m los lances efectuados con el OTSB-14 se segregaron (en un análisis MDS) de los lances realizados con el MTS-25, el CT, y el GOC73. La ordenación de los lances a lo largo del primer eje (DIM1) del MDS presentó una correlación significativa (r de Spearman) con la luz de malla en el sobrecopo, con la longitud de las mallas de los artes y con sus aberturas verticales. Al comparar los modelos CT y GOC73 con el MTS-25 las especies con mayor disimilaridad fueron *Aristeus antennatus*, *Galeus melastomus* y *Trachyrhynchus scabrus*. *A. antennatus* constituyó un caso particular con una densidad significativamente mayor en los lances de MTS-25 en comparación con el resto de artes utilizados. A 1200-1300 m los lances de OTSB-14 y de MTS-25 se segregaron en los análisis MDS. El segundo eje (DIM2) se correlacionó con el periodo de muestreo (mes), indicando un efecto estacional en la composición de especies. A 1200-1300

m la principal disimilaridad entre la composición del OTSB-14 y del MTS-25 vino marcada por *Alepocephalus rostratus* y por *A. antennatus* (capturados preferentemente con el MTS-25) y por *Cataetyx alleni*, por los Notacanthidae *Notacanthus bonapartei* y *Polyacanthonotus rissoanus*, y por *Plesionika acanthonotus* (capturados con el OTSB-14). En conclusión el OTSB-14 mostró una mayor abundancia en sus capturas que el MTS-25, el CT y el GOC73, mientras la *S* (número de especies) y la *J* (equitabilidad) fueron también significativamente más elevados en los lances con OTSB-14 que en los de MTS-25. En el talud inferior se encontró influencia del factor estacionalidad en la composición de peces y decápodos. Sin embargo, el MTS-25, con mayor abertura vertical que el OTSB-14, debe capturar *A. rostratus* de manera más eficiente dados los hábitos bentopelágicos de esta especie. Esto explica asimismo la mayor biomasa obtenida con el MTS-25 en este estrato. El MTS-25 seleccionó positivamente *A. antennatus*, coincidiendo con una capturabilidad negativa hacia otras especies.

Palabras clave: mar profundo, comparación de artes, diversidad, crustáceos decápodos, peces, *Aristeus antennatus*, OTSB.

INTRODUCTION

Information on the distribution of deep sea megafaunal (e.g. fish) assemblages and their diversity and abundance along depth gradients is still far from fully understood, especially considering that these aspects and their possible causes (e.g. trophic relationships) are relatively well known for only a few areas (e.g. Porcupine Seabight in the NE Atlantic, Merrett *et al.*, 1991a, b; Mid-Atlantic Ridge, Bergstad *et al.*, 2008). The marginal depths off the Iberian Mediterranean coasts (e.g. Balearic Basin, western Mediterranean) are among these reasonably well-known areas, and a considerable amount of information is available regarding the structure and dynamics of megafaunal-macrofaunal assemblages (Abelló and Valladares, 1988; Cartes and Sardà, 1993; Cartes *et al.* 1994; Stefanescu *et al.*, 1992, 1993; Maynou and Cartes, 2000, Abelló *et al.*, 2002), particularly trophic webs and trophic interrelationships among fishes (Macpherson, 1981; Carrassón and Cartes, 2002) and decapod crustaceans (Cartes, 1993; 1994). This work performed in the Balearic Basin has been recognised in recent reviews referring to “the active work developed by the group of Barcelona” (Tyler, 2003). Bathyal assemblages in the deep Mediterranean are dominated by two main taxa, fish and decapods, the latter well diversified with some species (e.g. *Aristeus antennatus*, *Acanthephyra eximia*, *Plesionika martia*) often reaching their northernmost distribution in the NW Mediterranean or at similar latitudes along NE Atlantic coasts (e.g. Cantabrian Sea, Bay of Biscay; (Lagardère, 1971; d’Udekem-D’Acoz, 1999; Cartes *et al.*, 2008). The dominance of decapods among invertebrates in the Mediterranean contrasts with the dominance of echinoderms in Atlantic waters at similar latitudes, as has been previously pointed out (Cartes and Sardà, 1993).

The deep Mediterranean is considered to be a natural laboratory (Margalef, 1985), due to its thermal (13°C) and saline (38 psu) stability below depths of only 150 m in the water column, though

long-term changes in oceanographic conditions have also been reported (Vargas-Yáñez *et al.*, 2009). Thus, environmental variability in areas such as the Catalan Sea slope seems low in comparison with other deep-sea areas. In addition to environmental variability, the type of collecting gear is another factor affecting the study of intra- and interannual changes in the composition and distribution of demersal bathyal assemblages (Merrett *et al.*, 1991a; Gordon and Bergstad, 1992; Bertrand *et al.*, 2002a). Selectivity among trawls depends on many variables, with mesh-size, mouth area, towing speed and the number of warps towing the net being the most important. Trawl comparisons have been analysed (e.g. by side-by-side trawling experiments) in shallow waters (Wilderbauer *et al.*, 1998; Szalay and Brown, 2001), basically for fisheries purposes. Similar studies have also been performed at bathyal depths (Percy *et al.*, 1982; Merrett *et al.*, 1991a, b; Gordon and Bergstad, 1992), more focused on ecological implications relating to biomass and size vs. depth distributions (Haedrich *et al.*, 1975; Percy *et al.*, 1982).

In the Balearic Basin the first ecological studies of bathyal communities were started between 1985 and 1992 by a team of researchers at the Institut de Ciències del Mar (ICM-CSIC) of Barcelona (Rucabado *et al.*, 1991; Stefanescu *et al.*, 1992, 1993; Cartes, 1993; Cartes and Sardà, 1993) using a 1-warp trawl, the OTSB-14. This is a standardised trawl in the study of deep-sea megafauna (Haedrich *et al.*, 1975; Gordon and Duncan, 1985; Merrett *et al.*, 1991b), particularly at depths below 1000 m, where 2-warp trawls are often difficult to use and manoeuvre. In 1991, a new 1-warp trawl system, the otter *Maireta trawl system*, with a headline of 25 m (MTS-25), was introduced in deep-water studies. MTS-25 specifications can be found in Sardà *et al.* (1997), who, after comparing selectivity of MTS-25 and OTSB-14 trawls based on a series of hauls performed at 1200 m, concluded that MTS-25 showed a better picture of sampled communi-

ties, catching mobile species more efficiently. This trawl was mainly introduced to improve catches of the red shrimp *Aristeus antennatus*, the main target species of deep-sea fisheries in the area, incorporating features of conventional commercial gear used by red-shrimp fishermen off the coasts of Catalonia (Sardà *et al.*, 1997). Other sources of ecological information have been obtained from the use of Agassiz trawls (Abelló and Valladares, 1988), commercial trawlers (Abelló *et al.*, 1988), and monitoring studies performed within the framework of MEDITS-Spain cruises (see Bertrand *et al.*, 2002b; Cartes *et al.*, 2002). MEDITS cruises have been performed along the Spanish coasts yearly in spring (May-June) since 1994, operating to ca. 800 m depth under the coordination of the Instituto Español de Oceanografía (IEO). As in the case of commercial trawlers, MEDITS cruises used a GOC73, a 2-warp system with the general design of a conventional commercial otter trawl (Bertrand *et al.*, 2002a, Fanelli *et al.*, 2007).

The aim of this study was to establish a comparison among trawls commonly used in studies on megabenthos in the deep, western Mediterranean in terms of: 1) species composition; 2) abundance/biomass; 3) species richness/diversity. We further discuss the biases introduced by each trawl in ecological aspects, such as zonation patterns and species distributions, and in the study of megabenthic biodiversity in bathyal habitats.

MATERIALS AND METHODS

The sampling area

We chose for our comparative study the area of the Catalanian coasts between Barcelona and the Ebro Delta, which has been the subject of many studies over the last 20 years. These sites are not under the direct influence of upwelling processes (local winds blowing in the Gulf of Lyons) (Fig. 1) and associated geological features (e.g. advective fluxes above large canyon: Palanques *et al.*, 2005). To remove the effect of depth gradients on assemblages, we compared hauls performed in two fixed bathymetric strata: 1) the mid-slope between 600 and 750 m, depths commonly worked by red-shrimp trawlers (Maynou, 2008); and 2) the lower slope between 1184 and 1320 m, depths which are free of any trawling activity.

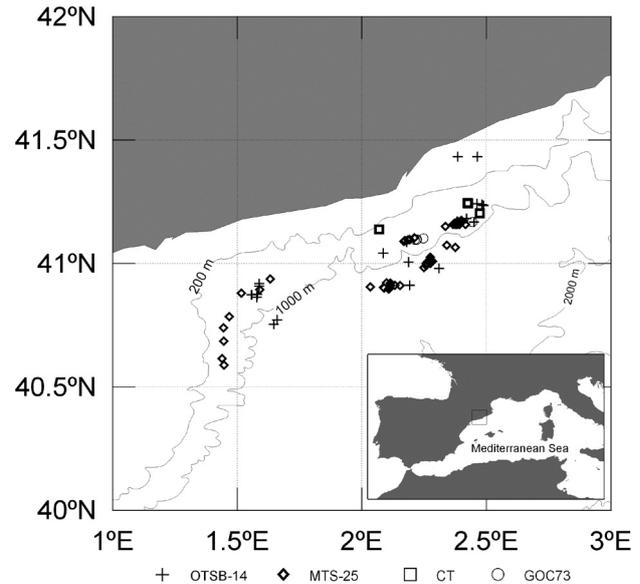


Fig. 1. – Map of the study area between Barcelona and Tarragona off the Catalan coasts.

The features of the trawls used are listed in Table 1. Together with the two 1-warp trawls used by ICM-CSIC teams (OTSB-14, MTS-25), and the GOC73 used by IEO on MEDITS cruises, we introduce data from a conventional trawler, the FV *Stella Maris III* operating in the harbour of Barcelona. The main differences among trawls were in the mesh size at the codend (6 to 40 mm), the length of bridles (8 to 150 m), and the vertical height or opening (1.2 to 3 m) (Table 1).

All hauls performed between 600 and 750 m and between 1184 and 1320 m, comprising a total of 57 hauls at 600-750 m and 32 hauls at 1184-1320 m, were selected for analysis. Hauls at 600-750 m were taken with four different trawls; on the lower slope only the two 1-warp models were used (OTSB-14 and MTS-25) (details in Table 1). Hauls came from cruises between 1988 and 1994 (BATIMAR, SPERMA, ZONAP, GEODELTA) and in 2007 (BIOMARE) using OTSB-14, between 1991 and 1995 (RETRO, BATMAN) using MTS-25, and between 2002 and 2007 (MEDITS-IEO). Commercial trawls were part of BIOMARE samplings in 2007.

Data analysis

Fish and decapods were counted and weighed by species and classified to species level in all cases both on board and in the laboratory.

Abundance and biomass (g wet weight/ha) were calculated by swept area after raw numbers (total in-

TABLE 1. – Main comparative characteristics of the four trawls used in the study area.

		OTSB-14	MTS-25	CT	GOC73
Vessel		<i>R/V García del Cid</i> 38 m, 1500 HP	<i>R/V García del Cid</i> 38 m, 1500 HP	<i>F/V Stella Maris</i>	<i>R/V Cornide Saavedra</i> 66.7 m, 1651 HP
No. samples taken	600-750 m	16	30	6	5
“	1100-1300 m	8	24	-	-
Year range		1988/1992 - 2007	1991/1995	2007	2002 - 2007
Months		Fe-Ap/May-Jun/Jul-Oc	Mar-Ap-Jun/Jul-De	Fe-Ap-May-Jun/Jul-De	May-Jun
Area covered (ha)		2.8-5.2	6.1-13.1	12.1-20.4	5.5-13.2
No. towing warps		1	1	2	2
Headline length (m)		14	25	50	35.7
Bridle length (m)		8	25	150	30
Wing mesh size (mm)		44	80 (<i>stretched</i>)	-	140 (<i>stretched</i>)
Codend mesh size (mm)		6	10 (<i>stretched</i>)	40	20 (<i>stretched</i>)
Horizontal length (m)		6.7-7.2	13.5	25	18
Vertical height (m)		1.2	2	3	2.7
Median towing speed (knots)		2.6-2.7	2.6-2.8	2.4-2.5	2.8-2.9

dividuals collected per haul) had been standardised to individuals per hectare. Horizontal length (m) recorded by SCANMAR devices mounted on wing trawls, median towing speed (knots) and haul duration (h) were used to calculate swept area.

Multidimensional scaling (MDS) was performed on matrices of data similarities. Two distances were used for the middle slope, the quantitative Bray-Curtis distance after log-transformation of data (Clarke and Warwick, 1995), and the non-parametric Spearman's correlation coefficient, a rank-based measure. Bray-Curtis was the only distance used for the lower slope data, because both measures showed basically the same trends. Fishes and decapods were analysed together, while non-arthropod invertebrates were excluded from analyses because trawling is not a suitable method for quantifying epibenthic and infaunal invertebrates. As a consequence, variations found in epifaunal-infaunal catches cannot be due only to natural variations, but depend on the unpredictable behaviour of trawls collecting these non-swimming, often buried, species. PERMANOVA analyses (one factor, trawls; 999 permutations) were performed on a fish and decapod resemblance matrix (Bray-Curtis distance) to test the significance of groups formed in MDS analyses. SIMPER was performed to establish the contribution of each species to dissimilarities between the types of trawl. Factors (trawls) were the four types of trawl employed (CT, OTSB-14, MTS-25, GOC73).

Spearman's correlations were calculated between MDS dimensions and a number of variables likely a priori to influence the species composition per trawl. The following variables were considered:

i) Technical variables: mesh size at codend, trawl height (vertical opening) and bridle length (see Table 1)

ii) Natural variables: latitude (LAT) and longitude (LONG) to define the fishing grounds or areas, time of the day (h, GMT), intrannuality (month) and interannuality (year) of samples. Intrannuality of surveys was distributed as follows: BATHOS (June-July, October 1988), SPERMA (October 1989), ZONAP (May 1992), GEODELTA (May 1994), RETRO (April-December 1991, March-July 1992), BATMAN (March 1994, June 1995) and BIOMARE (January 2006 to February, April-May, June-July and October 2007). A rank order was assigned per month as a function of increasing duration of daylight at the latitude studied (e.g. 1 for December, 12 for June). MEDITS were performed between 2002 and 2007, always in May-June.

iii) Measures of species diversity: number of species (N), Shannon index (H') and evenness (J).

Differences in biomass per trawl were tested by 1-way ANOVA (after log-transformation of data) for total biomass and for the main dominant species of fishes and decapods. Mean weight per haul (biomass/number) was calculated for key species having the greatest contribution to dissimilarities (e.g. *Aristeus antennatus*; *Alepocephalus rostratus*), and differences among trawls were tested by 1-way ANOVA.

Measures of diversity (H , Shannon-Weaver index), evenness (J , Pielou) and species richness (S) per haul were calculated. Differences of mean S , H and J were tested among gear types by 1-way ANOVA. We performed the Wilcoxon paired-

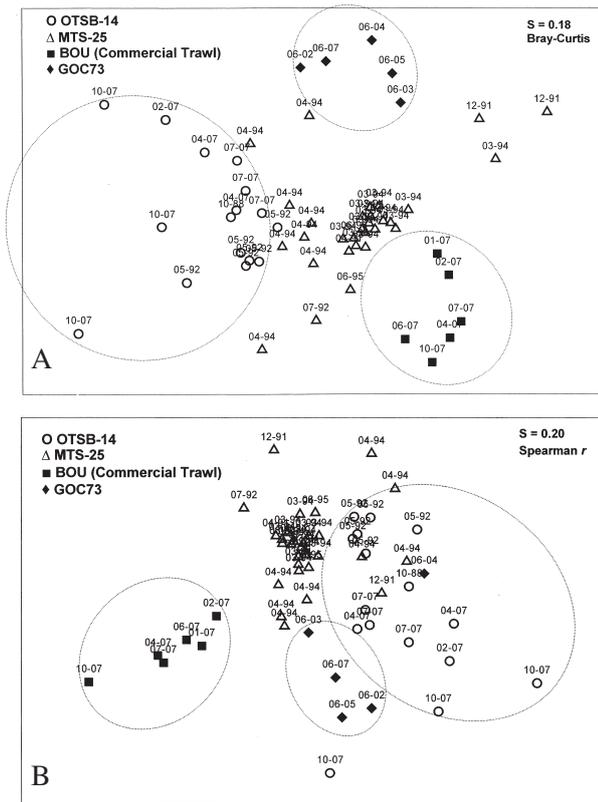


Fig. 2. – MDS (multi-dimensional scaling) analysis for fish and decapods collected with four bottom trawls at 600-750 m. A, Bray-Curtis distance; B, nonparametric Spearman's *r*. Labels indicate month and year of sample.

match test to establish whether the differences between each set of pairs of species abundance per trawl were significantly different from the expected 50% of switches between trawls in the absence of significant bias. We used Mann-Whitney tests to evaluate paired comparisons of species abundance from gear to gear. All the analyses were performed using PRIMER6 & PERMANOVA+ (Clarke and Warwick, 1995; Anderson, 2001) and STATISTICA 7.0 software.

RESULTS

Species composition

600-750 m depth range

Based both on Bray-Curtis and on Spearman's *r* distances, MDS showed similar aggregations of hauls as a function of the trawl type (Fig. 2A). Based on Bray-Curtis, the OTSB-14 hauls (on the

left side of the plot) were separated from the MTS-25, CT and GOC73 hauls. The six hauls performed with commercial trawls (CT) and the five GOC73 hauls were grouped together. On DIM 1 (horizontal axis), the MTS-25 hauls were on average closer to the CT hauls, and to a lesser extent to GOC73, than to the OTSB-14 hauls. Average trawl composition differed significantly between the 4 trawls used (PERMANOVA test: pseudo $F=7.44$, $P=0.001$; post hoc tests, $P<0.01$ between all paired comparisons). Based on Spearman's rank correlation, segregation between the OTSB-14 and GOC73 hauls was not as evident as using Bray-Curtis; GOC73 hauls occupied an intermediate position between the OTSB-14 and MTS-25 hauls in MDS. CT hauls were clearly aggregated and separated from the other hauls (Fig. 2B).

1200-1300 m depth range

The OTSB-14 and MTS-25 hauls were clearly segregated (significantly different composition) in the MDS plot (Fig. 3) performed on the Bray-Curtis distance. (PERMANOVA test: pseudo $F=4.75$, $P=0.001$).

Abundance, biomass and diversity

600-750 m

A 1-way ANOVA performed on total abundance of megafauna after data standardisation to area swept (ind./ha) showed significant changes in abundances as a function of trawl type ($F=5.93$, $P=0.001$). Abundance of fauna caught with OTSB-14 was sig-

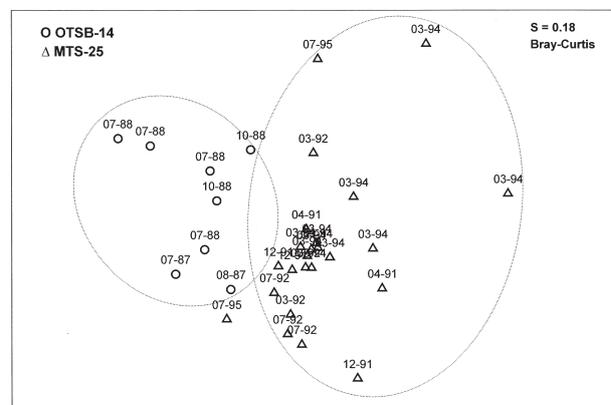


Fig. 3. – MDS (multi-dimensional scaling; Bray-Curtis distance) analysis for fish and decapods collected with the two 1-warp bottom trawls at 1150-1350 m. Labels indicate month and year of sample.

TABLE 2. – 1-way ANOVA and t-test results at 600-750 m and at 1200-1350 m with paired post-hoc comparisons (Scheffé) for the shallower stratum. *N*, species richness; *H'*, diversity, Shannon's index; *J*, evenness; *D*, density; *B*, biomass, *n*, number of hauls.

	600-750 m				1-way ANOVA		Scheffé
	CT	OTSB-14	GOC73	MTS-25	<i>F</i>	<i>p</i>	
<i>D</i> (ind/h)	36.8	138.5	39.6	61.8	5.95	0.001	CT vs OTSB-14 <i>p</i> =0.03; OTSB-14 vs MTS-25 <i>p</i> = 0.008
<i>B</i> (g/ha)	1762.0	1715.1	1854.6	1988.3	0.36	<i>ns</i>	<i>ns</i>
<i>N</i>	31.5	33.8	36.0	29.1	4.06	0.01	OTSB-14 vs MTS-25 <i>p</i> = 0.04
<i>H'</i>	1.03	1.22	1.11	1.05	2.09	0.11	<i>ns</i>
<i>J</i>	0.69	0.80	0.72	0.73	4.42	0.008	OTSB-14 vs MTS-25 <i>p</i> = 0.01
<i>n</i>	6	16	5	30			

	1200-1300 m		t test	
	OTSB-14	MTS-25	<i>F</i>	<i>p</i>
<i>D</i> (ind/h)	46.2	67.3	4.03	0.054
<i>B</i> (g/ha)	1548.6	4695.1	19.29	0.0001
<i>N</i>	23.8	24.5	0.24	<i>ns</i>
<i>H'</i>	1.01	0.97	1.28	<i>ns</i>
<i>J</i>	0.74	0.70	3.70	0.064
<i>n</i>	8	24		

nificantly greater than with MTS-25 (Scheffé test; $P=0.008$) (Table 2). The biomass per swept area obtained with OTSB-14 was slightly less than for the other three trawls, but without any significant difference among the trawls (1-way ANOVA: $F=0.36$; $P=0.78$) (Table 2).

A 1-way ANOVA performed on *S* (species richness), showed higher *S* for OTSB-14 than for MTS-25 ($F=4.06$, $P=0.01$; Scheffé test, $P=0.04$) (Table 2), while differences between MTS-25 and GOC73 *S* were close to the significance level. Shannon's *H'* diversity was also higher for OTSB-14 than for MTS-25 (Scheffé test, $P=0.013$; Table 2), while no significant differences among trawl type were obtained for Pielou's (*J*) equitability (Table 2),

1200-1300 m

One-way ANOVA performed on *S*, *H'* and *J* did not indicate significant differences between the MTS-25 and OTSB-14 trawls. Significant differences were not found for total density (*D*), although *D* in MTS-25 hauls was higher and close to statistical significance ($P=0.05$). Biomass was significantly higher in the MTS-25 hauls (Table 2).

Correlations between MDS dimensions and related variables

600-750 m

Bray-Curtis MDS. Spearman's rank correlations indicated significantly positive relationships between DIM1 values from the MDS (Fig. 2) and mesh size

($r=0.718$; $p<10^{-6}$), which is consistent with the respective positions of the CT hauls (mesh size = 40 mm) and GOC73 (mesh size = 20 mm) and the OTSB-14 hauls (mesh size = 6 mm) on opposite sides of the plot. In parallel, we found similarly significant relationships ($r=0.791$; $P<10^{-6}$) regarding other technical features of trawls (bridle length, opening height), with the highest trawls having the largest bridles and OTSB-14, with the lowest vertical opening and the shortest bridle, occupying opposite positions in the MDS plot (Fig. 2A). Furthermore, the trawl-characteristic variables *H'* ($r=-0.384$; $p=0.003$) and *J* ($r=-0.513$; $P=4 \cdot 10^{-5}$) were negatively correlated with DIM1; that is, diversity was higher in the OTSB-14 hauls. Finally, DIM 1 was almost significantly correlated ($P=0.05$) with LAT. This is because GOC73 and CT were exclusively performed off Barcelona, at the northernmost latitudes in our sampling area. The latitudinal effect was weak because these southernmost hauls (GE hauls, off the Ebro Delta) were not situated to the left along DIM1. DIM2 positions were not correlated with any variable.

Spearman's MDS. Similar results to those for Bray-Curtis were found for the rank-criterion ordination of hauls. DIM1 values were correlated with mesh size (-0.557 ; $P=7 \cdot 10^{-6}$) and with both bridle length and opening height ($r=-0.634$; $P<10^{-6}$), whereas *J* again was greater in OTSB-14/GOC73 hauls ($r=0.329$; $P=0.01$). DIM2 was weakly correlated with LONG ($P=0.05$) and also with bridle length ($r=-0.540$; $P<1 \cdot 10^{-5}$).

No significant correlations between year and month of sampling and DIM of MDS analyses (either for Bray Curtis and Spearman distances) were found.

1200-1300 m

Bray-Curtis MDS. For the lower slope trawls, we did not test mesh size, bridle length or opening height as explanatory variables, because we had only one source of variation (MTS-25 vs. OTSB-14 trawls). Species number, S , was positively correlated with DIM1 (Fig. 3; $r=0.389$; $P=0.02$, i.e. higher S on average for hauls situated to the right). This does not mean, however, that S was higher among MTS-25 hauls, because MTS-25 and OTSB-14 hauls were clearly separated along DIM1, whereas S was not significantly correlated with this axis. DIM1 was also negatively correlated with J ($r=-0.409$; $P=0.02$).

DIM2 was correlated with month of sampling ($r=-0.356$; $P=0.04$). Most MTS-25 hauls were in March-April, while OTSB-14 hauls were mainly performed in June-July and October. No significant correlations were found regarding the year of sampling or MDS dimensions.

SIMPER results: species contribution by trawl types

Considering only those species contributing $\geq 5\%$ of d , higher similarities between species composition (less d) were found in the comparison of GOC73 vs OTSB-14 ($d=30.8\%$) and CT vs MTS-25 ($d=42.5\%$). In both cases, higher similarities were found in paired comparisons between 1- and 2-warp trawls than between the two 1-warp trawls ($d=43.1\%$) or the two 2-warp trawls ($d=59.0\%$).

600-750 m

When the trawls with the two largest mesh sizes at the codend (CT and GOC73) were compared with OTSB-14, the species contributing most to dissimilarities (d) according to SIMPER analysis (Table 3) were small crustaceans such as *Calocaris macandreae*, *Munida tenuimana* and *Sergestes arcticus*.

TABLE 3. – SIMPER analysis results by depth strata and comparing (average dissimilarity) trawl by trawl. CT, commercial trawl.

600-750 m	CT/OTSB-14 species	Av.Diss	Av Diss = 73.2 %Contrib	GOC73/OTSB-14 species	Av.Diss	Av Diss = 73.2 %Contrib
	<i>Calocaris macandreae</i>	7.45	10.17	<i>Calocaris macandreae</i>	7.31	10.19
	<i>Munida tenuimana</i>	6.27	8.56	<i>Plesionika martia</i>	5.59	7.79
	<i>Sergestes arcticus</i>	4.88	6.67	<i>Munida tenuimana</i>	4.86	6.78
	<i>Plesionika martia</i>	4.75	6.48	<i>Sergestes arcticus</i>	4.36	6.08
	<i>Plesionika acanthonotus</i>	4.05	5.53	<i>Plesionika acanthonotus</i>	3.96	5.52
	<i>Polycheles typhlops</i>	3.82	5.21			
CT/MTS-25 species	Av.Diss	Av Diss = 56.5 %Contrib	GOC73/MTS-25 species	Av.Diss	Av Diss = 73.7 %Contrib	
	<i>Aristeus antennatus</i>	15.54	27.5	<i>Aristeus antennatus</i>	15.18	25.13
	<i>Nephrops norvegicus</i>	4.04	7.14	<i>Galeus melastomus</i>	4.5	7.45
	<i>Trachyrhynchus scabrus</i>	2.6	4.8	<i>Trachyrhynchus scabrus</i>	4.44	7.34
				<i>Lampanyctus crocodilus</i>	4.17	6.9
				<i>Geryon longipes</i>	3.53	5.84
CT/GOC73 species	Av.Diss	Av Diss = 65.3 %Contrib	OTSB-14/MTS-25 species	Av.Diss	Av Diss = 61.0 %Contrib	
	<i>Trachyrhynchus scabrus</i>	9.35	14.31	<i>Aristeus antennatus</i>	8.14	13.34
	<i>Phycis blennoides</i>	6.08	9.31	<i>Calocaris macandreae</i>	5.55	9.1
	<i>Lampanyctus crocodilus</i>	5.69	8.71	<i>Munida tenuimana</i>	5.13	8.4
	<i>Nephrops norvegicus</i>	5.01	7.67	<i>Sergestes arcticus</i>	3.88	6.35
	<i>Geryon longipes</i>	4.98	7.62	<i>Plesionika martia</i>	3.59	5.89
	<i>Galeus melastomus</i>	4.1	6.27			
1200-1300 m	OTSB-14/MTS-25 species	Av.Diss	Av Diss = 36.2 %Contrib			
	<i>Alepocephalus rostratus</i>	3.34	9.21			
	<i>Trachyrhynchus scabrus</i>	2.1	5.79			
	<i>Nezumia aequalis</i>	2.09	5.78			
	<i>Bathypterois mediterraneus</i>	2.03	5.6			
	<i>Pontophilus norvegicus</i>	1.81	5			
	<i>Cataetyx alleni</i>	1.79	4.93			
	<i>Plesionika acanthonotus</i>	1.76	4.86			
	<i>Aristeus antennatus</i>	1.74	4.79			
	<i>Acanthephyra eximia</i>	1.59	4.39			
	<i>Mora moro</i>	1.49	4.1			
	<i>Polyacanthonotus rissoanus</i>	1.45	3.99			

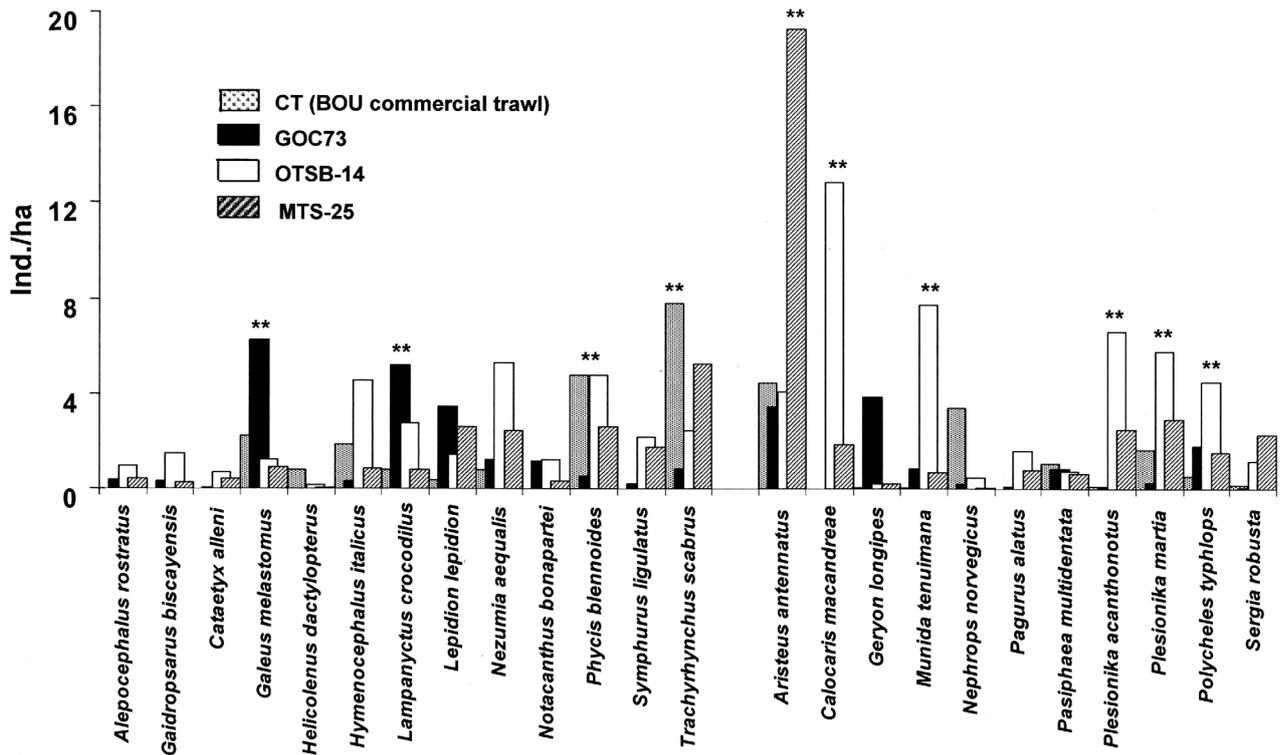


Fig. 4. – Dominant species of fishes and decapods as a function of gear at mid-slope depths (600-750 m). Asterisks (**) above species indicate that differences in catchability were significant among trawls.

When CT and GOC73 were compared with MTS-25, however, the most dissimilar species were not small species, but large ones such as *Aristeus antennatus*, *Galeus melastomus* and *Trachyrhynchus scabrus*. A particular case was *Aristeus antennatus*, for which d was greater between MTS-25 and the large 2-warp trawls (CT and GOC73, respectively 15.2-15.7%) than between MTS-25 and OTSB-14 (8.1%).

1200-1300 m

At 1200 m the main dissimilarities between OTSB-14 and MTS-25 were marked by *Alepocephalus rostratus* and *Aristeus antennatus* being caught mostly with MTS-25, and by *Lepidion lepidion* and *Munida tenuimana* being mainly caught with OTSB-14 (Table 3).

Species-by-species abundance per trawl type

600-750 m

A species-by-species, 1-way ANOVA showed significantly higher abundance of *Aristeus antennatus* when it was collected with an MTS-25 than

with an OTSB-14 (Scheffé test; $P < 0.001$) or the CT ($P < 0.05$; (Fig. 4). Other species showed significantly different catchability depending on the trawl used. Other decapods showing such differences were *Calocaris macandreae* (higher catchability with OTSB-14 than with GOC73 or CT, $P < 0.001$), *Munida tenuimana* (higher catchability with OTSB-14 than with GOC73, $P < 0.05$, and greater with MTS-25 than with CT, $P < 0.001$), *Plesionika acanthonotus* (higher catchability with OTSB-14 than with GOC73 or CT, $P < 0.01$; higher catchability with MTS-25 than with CT, $P < 0.05$), *Plesionika martia* (higher catchability with OTSB-14 than with GOC73 or MTS-25, $P < 0.01$) and *Polycheles typhlops* (higher catchability with OTSB-14 than with MTS-25 or CT, $P < 0.01$). In general most of these differences are attributable to the smaller mesh size of OTSB-14 in comparison with the two 2-warp trawls. However, differences between OTSB-14 and MTS-25 for mid-sized species, such as *Plesionika martia* and *Polycheles typhlops*, cannot be explained by mesh-size differences alone. Among fish, *Galeus melastomus* showed significantly higher abundance with GOC73 than with OTSB-14 ($P > 0.01$), while MTS-25 showed lower catching efficiency than

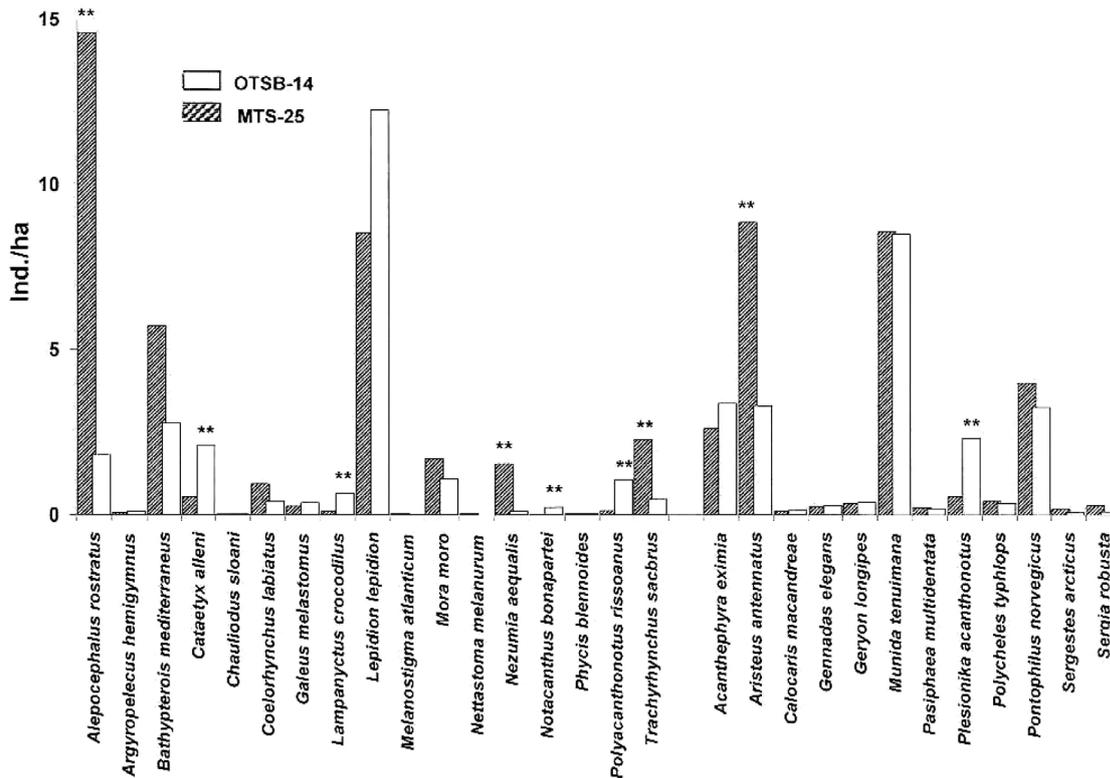


Fig. 5. – Dominant species of fishes as a function of gear at the lower slope depths (1200-1300 m). Asterisks (**) above species indicate that some differences in catchability were significant among trawls.

GOC73 ($P < 0.001$) and CT ($P < 0.05$). *Lampanyctus crocodilus* showed lower catchability with MTS-25 than with either OTSB-14 ($P < 0.001$) or GOC73 ($P < 0.05$). *Phycis blennoides* showed significantly lower catchability with GOC73 ($P < 0.05$) than with CT. *Trachyrhynchus scabrus* was collected in greater numbers with CT than with the other trawls ($P < 0.01$), and more were caught with MTS-25 than with OTSB-14 ($P < 0.05$).

Comparing catches of the two 1-warp trawls, a significant number of species showed greater abundance in the OTSB-14 hauls ($n=19$) than in the MTS-25 hauls ($n=4$) (Wilcoxon paired-matched test was significantly different from the expected 50% in the absence of any significant effect, $P > 0.001$). No significant trends were found between the two 2-warp systems.

1100-1300 m

Some fishes showed higher catchability with MTS-25 (Fig. 5): *Alepocephalus rostratus* (t test, $P < 0.001$), *Nezumia aequalis* ($P < 0.001$) and *Trachyrhynchus scabrus* ($P < 0.01$) together with *Aristeus antennatus* ($P < 0.01$). On the other hand, *Cataetix*

alleni ($P < 0.001$), *Lampanyctus crocodilus* ($P < 0.05$) and the notacanthids *Notacanthus bonapartei* and *Polyacanthonotus rissoanus* ($P < 0.05$) were more readily caught by the OTSB-14. The same trend was found for the shrimp *Plesionika acanthonotus* ($P < 0.05$). All these comparisons, however, could be biased by seasonality.

The number of species collected more effectively by MTS-25 was not significantly different from the number collected better by OTSB-14 (Wilcoxon paired-matched test).

DISCUSSION

Our approach was based on trawl series performed in two relatively narrow depth ranges (600-750 m and 1200-1300 m) in a homogeneous area over a period of ca. 20 yrs. Though it was not a side-by-side trawling experiment, as performed at shelf depths (e.g. by Szalay and Brown, 2001), similar approaches combining data from different surveys have been applied at bathyal depths (e.g. in the North Atlantic: Merrett *et al.*, 1991a, b) due to the limitations of performing trawl and side-by-side surveys at great depths.

Natural and human-induced variability

Previous studies on muddy, bathyal bottoms off the Iberian coasts showed significant changes in megafaunal assemblages at the spatial mesoscale (latitude: Cartes *et al.*, 2002) with an effect of the mainland/island factor (Cartes *et al.*, 2004). Trophic guilds of decapods and fish varied along the Spanish Mediterranean coasts from Catalonia to the Straits of Gibraltar, with a north to south increase in plankton feeders. Also, around insular areas in the Iberian Mediterranean coasts, low advective fluxes (e.g. river discharges) and the impoverishment of benthic biomass are characteristic (Cartes *et al.*, 2004), enhancing differences between insular and mainland bathyal communities. As latitude was not correlated with species composition in our MDS analyses, we can consider the geographic area selected as homogeneous for our purpose.

Anthropogenic factors, mainly fisheries, may also influence the composition of megafaunal assemblages in the study area. The trawler fleet has moved deeper (to *ca.* 900 m) in search of *Aristeus antennatus* in recent years off the Catalan coasts, though the influence of trawling on communities is nil below 900 m depth (Cartes *et al.*, 2004), and the lower slope at 1200-1300 m must be considered as a pristine area. *Isidella elongata*, a soft-coral forming a characteristic facies in the deep Mediterranean (Pérès, 1985), which is inhabited by important commercial species (the large red-shrimps *Aristeus antennatus* and *Aristaeomorpha foliacea*), is immediately removed from fishing grounds by trawling. Habitat generated by *Isidella* enhances diversity of fish and especially of decapods, some of them living as epibionts on coral colonies (author's unpubl. data). Geodelta survey (GE) hauls were the only ones performed in pristine areas at 600-750 m, while the rest were from fishing grounds of the red shrimp *Aristeus antennatus*. However, the massive occurrence of *Isidella elongata* colonies (author's unpubl. data) in GE hauls cannot influence our analyses performed only on fish and decapods (GE hauls not segregated from the rest performed on fishing grounds in MDS analyses).

Other sources of variability in deep-sea communities are related to temporality (Tyler, 1988). In the deep Mediterranean, seasonality strongly influences the dynamics of benthopelagic communities (Cartes, 1998; Cartes *et al.*, 2008), trophic relationships and food consumption (Cartes, 1994; Madurell and

Cartes, 2005), and the biological cycles of bathyal species, both macrofauna and megafauna (Cartes and Sorbe, 1996; Fanelli and Cartes, 2008). Though seasonality (= month) had no significant effect on trawls from the 600-750 m stratum, it significantly influenced the species composition at 1200-1300 m, so trends observed in that stratum can be biased by natural variability and fluctuations of biomass, in addition to trawl characteristics. Seasonal fluctuations in abundance were evident in the study area on the lower slope (Sardà *et al.*, 1994). Compared with a previous study (Sardà *et al.*, 1997), in which the lack of any seasonal effect was assumed, we found some seasonal influence on species composition after comparing MTS-25 hauls (performed between 1991 and 1995 mainly in March and April) with OTSB-14 hauls (performed in 1988-1989 mainly in June-July and October).

Trawl type variability

The main trend in the comparison of assemblage composition using different trawls was the sharp bias introduced by MTS-25 in the catches of *Aristeus antennatus* (i.e. >4 times higher than OTSB-14 catches) both at 600-750 and at 1200-1300 m. This positive selectivity of red shrimp by MTS-25 was also found when it was compared with 2-warp trawls, i.e. commercial hauls. It is well known that *A. antennatus* has strong interannual fluctuations in abundance, and in some years it even disappears from the fishing grounds (Maynou, 2008). Landings at the harbours of Barcelona and Vilanova were especially high in 1991-1992, whereas they decreased to *normal* or *average* catches in 1994-1995 (Maynou, 2008). Therefore, the peak of *A. antennatus* in 1994-95 using an MTS-25 trawl did not coincide with landing changes. The presumably low catches in 1992 with an OTSB-14 even coincided with a peak in landings. Thus, the differences observed were not related to fluctuations in red shrimp abundance but to the type of gear used.

On the lower slope a similar trend of higher catches with MTS-25 was found for the fish *Alepocephalus rostratus*, in agreement with previous analyses (Sardà *et al.*, 1997; Moranta *et al.*, 1998). Sampling with trawls of different opening height gives ecological information on the distribution of species close to the bottom (Engås and Godø, 1986). *A. rostratus* feeds on gelatinous plankton (medusae, pyrosomids: Carrassón and Cartes, 2002) at 1200 m depth, so

its benthopelagic behaviour may favour avoidance of trawls with a low opening height like OTSB-14. This trawl opens 1.2 m vertically (as SCANMAR systems record) on average (cited as 2 m by Sardà *et al.*, 1997). Because MTS-25 opens to 2 m, we can conclude that most *A. rostratus* biomass occurs well above one metre from the bottom. Such biases may change the apparent bathymetric location of peaks of biomass, especially in swimming or bathypelagic animals (Merrett *et al.*, 1991a). Gordon and Bergstad (1992) have shown that fast-swimming species (e.g. squalid sharks and alepocephalids) were more abundantly caught by a wider trawl operated at higher trawling speeds. We think estimates of *A. rostratus* abundance mainly depend on the opening height of trawls used.

Codend mesh size is one of the main factors explaining differences in species composition using different trawls (Merrett *et al.*, 1991a). Despite the small (10 mm) mesh of the MTS-25 codend, the greatest dissimilarities were observed when MTS-25 was compared with 2-warp trawl catches. These larger differences were not found among small species, as expected, but among medium and large-sized species (e.g. sharks and macrourids). In addition, medium-sized species, such as the fish *Lepidion lepidion* and the shrimp *Acantheephyra eximia*, were caught in significantly greater numbers using an OTSB-14 than an MTS-25. This suggests that MTS-25 is selective for most species, probably because it was designed specifically for a commercial species, the red shrimp. In contrast to *Alepocephalus rostratus*, positive selectivity of MTS-25 for *Aristeus antennatus* in comparison with OTSB-14 is unrelated to swimming capacity, because i) the red shrimp diet off the Catalan coasts is mainly infauna and suprabenthos (Cartes, 1994), which are distributed at 0-1 m above the bottom, and ii) similar yields were obtained for *A. antennatus* using an OTSB-14 and 2-warp trawls (CT/GOC73) with opening heights of ca. 3 m. As MTS-25 does not catch smaller species/specimens than commercial trawls, it probably enhances bigger-deeper trends when it is used across wide bathymetric ranges.

In terms of species richness and diversity, OTSB-14 behaved better than MTS-25 at 600-750 m, with higher *S* and *H'*. Surprisingly, diversity of MTS-25 hauls was no greater than that of 2-warp trawls. This can also be explained by the highly positive selectivity of MTS-25 towards *Aristeus antenna-*

tus (see Fig. 4), because the high dominance of a single species reduces *H'* values. Different trawls also increase artifactual variability when patterns found in different areas are compared, e.g. in studies of zonation. For example, Maynou and Cartes (2000) found differences in zonation for decapod crustaceans collected in the Algerian Basin from patterns previously found in the Catalano-Balearic Basin by Cartes and Sardà (1993); the former study was performed with MTS-25, the latter with OTSB-14. Differences mainly consisted in a lack of renewal of assemblages at around 1200 m off the Algerian Basin (Maynou and Cartes, 2000). Most species of decapod crustaceans are present in both the Balearic and Algerian Basins (e.g. both mainland and insular areas: Cartes *et al.*, 2004; Massutí and Reñones, 2005). Although different food availability in the two areas explains differences in species composition, the 1200-1300 m boundary coincided in the Catalan Sea with significant changes in the population structure and biomass of *Aristeus antennatus* (Sardà and Cartes, 1993), and other decapods. Thus, biases introduced by differing trawl effectiveness, which are species-dependent, can affect the centres of gravity of species and the zonation patterns reported in the literature.

In conclusion, we have shown that at mid-bathyal depths off the Catalanian coasts OTSB-14 is an effective trawl for community studies, showing significantly greater abundance estimates than MTS-25, CT and GOC73, and greater diversity (both *H'* and *S*) than MTS-25. The OTSB, often considered as an adequate megafaunal sampler at great depths (>1000 m) (Rucabado *et al.*, 1991), also gave acceptable results for biomass (non-significantly lower values than MTS-25 and the two 2-warp systems) at 600-750 m. On the lower slope seasonality influenced trawl comparisons; however, it seems reasonable to consider that MTS-25, with greater opening height than OTSB-14, was better at catching the benthopelagic fish *Alepocephalus rostratus*. The greater biomass obtained by MTS-25 on the lower slope is mainly attributable to this species. MTS-25 positively selected the red shrimp *Aristeus antennatus*, and it seemed that this positive selection was parallel to negative selection for other species of fish and decapods, giving a more biased picture of species composition than the other samplers. OTSB-14 seems to be the most suitable system for the study of some trends in deep-sea ecology, particularly regarding diversity.

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