Fuzzy diel patterns in catchability of deep-water species on the continental margin

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Exploited deep-water fish communities on continental margins are poorly understood in terms of variations in species composition and abundance by depth and season as a response to diel changes in light intensity and length of photoperiod. Innovative fuzzy clustering and traditional agglomerative hierarchical clustering methods were applied to data from bottom trawls collected continuously for 4 d in October and June, on the shelf (100–110 m) and upper slope (400–430 m). Fuzzy clustering was more effective than hierarchical clustering at characterizing diel variations in catches from the upper slope because the species assemblage did not show a distinct day and night structure. On the shelf, the species assemblages shifted abruptly between a diurnal and a nocturnal structure at sunset and sunrise, and the two clustering methods yielded similar results. Endobenthic decapods with marked crepuscular-nocturnal emergence from the substratum were mostly responsible for this pattern. No clearly discernible diel pattern was found with the dampening of light intensity with depth, weakening the behavioural response of endobenthos to the day–night cycle. The results indicated that the regulatory effect of the light cycle on diel activity rhythms weakens with depth.

Keywords: bottom trawl catches, catch assessment surveys, fuzzy clustering, hierarchical clustering, Mediterranean Sea, multispecies fishery.

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Introduction

Biological rhythms are widely reported for resources of the continental shelf and margins of all oceans (Naylor, 2005). Species display behavioural responses to fluctuations in light intensity that result in the movement of thousands of individuals through different depth strata of the water column, seabed depths, or in and out of the sediment (see review by Aguzzi *et al.*, 2008b). At a community level, the synergistic interaction of behavioural rhythms exhibited by the constituent species creates marked temporal variations in the assemblages detected by trawling at different hours in different depths (Engås and Soldal, 1992; Casey and Myers, 1998; Godø *et al.*, 1999). Unfortunately, the variations in catchability and species assemblages at different depths, depending on hour and day of the season, are still poorly characterized (Naylor, 2005).

Trawling is technically the most effective method for population assessment in deep-water continental margins (Raffaelli *et al.*, 2003). Stock assessment studies rely on trawling data for population demographics and distribution estimates, but because of activity rhythms, these data may be biased when sampling takes place with no cognizance for time of day (Aguzzi and Sardà, 2008). Misinterpretations of community structure are likely when catches are not taken by day and by night at the same location (Lleonart, 1993; Abelló *et al.*, 2002; Brander, 2003; Lleonart and Maynou, 2003). Detecting and exploring diel variations in trawl catches of species is helpful in improving the performance of assessment and selectivity experiments, as is conducting catch surveys for model validation (Casey and Myers, 1998; Hjellvik *et al.*, 2001, 2002).

Hierarchical clustering is a method often used to explore diel and seasonal variations in the abundance of some commercial species qualitatively (Lloret *et al.*, 2000; Sardà *et al.*, 2002; Carpentieri *et al.*, 2005). It is a conventional multivariate statistical technique that identifies homogeneous subgroups within a population (Zar, 1984). The method assigns absolute group memberships to clusters defined by rigid boundaries; objects can belong to just one group. This may represent a limitation in studies focusing on diel variations in the community structure as determined by trawling when catches are made at day–night transitions or at different depths. In contrast, fuzzy classification is based on membership grades, not absolute membership (Zadeh, 1965), so objects can belong to more than one group at the same time, with the sum of all their membership grades equal to one. Fuzzy classification has potential application in biological and ecological studies by bringing out discontinuities among groups rather than constraining groups within rigid boundaries (Dunn, 1973; Silver, 1997; Nicholls and Tudorancea, 2001; Schaefer and Wilson, 2002). Although the method possesses potential advantages for characterizing diel variations in the composition and abundance of species in trawl catches performed at different times of day, the power of the methodology has not yet been tested in field studies of economically and ecologically important continental margin communities. Regression analyses of patterns in diel variations of catch rates from bottom-trawl surveys have been reported with the use of generalized additive models (Adlerstein and Ehrich, 2003) and generalized linear models (Benoît and Swain, 2003).

In this study, fuzzy clustering was used as a method of characterizing the diel variation in the abundant commercially important species that inhabit shelves and slopes of the northwestern Mediterranean. We analysed trawl catch data obtained over several consecutive days of repeated trawling in two depth strata in two different seasons; in October, close to the autumn equinox, and in June, close to the summer solstice. Fuzzy analysis was used to measure the effects that day–night and seasonal variations in the length of the photoperiod may exert on commercial catches and scientific sampling. Traditional hierarchical clustering was also applied to the data and compared with the results of the fuzzy analysis to assess the contribution of the fuzzy clustering approach to characterizing variations in the diel patterns in species assemblages.

Methods

Data collection

Data were collected according to the methodology described by Aguzzi *et al*. (2003). Briefly, two research cruises were made to the northwestern Mediterranean during two seasons (Table 1); close to the autumn equinox (with ~12 h of daylight and 12 h of darkness) from 28 September to 8 October 1999, and close to the summer solstice (with daylight well exceeding darkness) from 22 June to 3 July 2000. Two depths were investigated, one on the continental shelf (100–110 m) off the Ebro delta (latitude and longitude ranges: 40°39′N 1°13′E; 40°38′N 1°11′E), and the other on the upper slope (400–430 m) off Tarragona (41°01′N 01°37′E; 40°55′N 01°31′E). Trawling was continuous for 4 d along the same transect at each depth. In October, 32 hauls were made on the shelf and 34 on the upper slope. In June, 34 hauls were performed on both shelf and upper slope. Surveys were carried out on board the RV "Garcia del Cid" (38 m long, 1200 hp) equipped with an otter trawl of vertical mouth opening 1.4–1.6 m (OTMS; Sardà, 1998). The net opens immediately above the seabed during towing, but the mouth closes when the gear is lifted off the seabed, so there is no chance of contamination of bottom catches with pelagic organisms (Sardà, 1998). Nominal towing duration was 90 min for shelf surveys and 60 min for upper slope surveys. All surveys were carried out using the same vessel and gear and under comparable technical conditions to the extent possible.

Data processing

For the analysis, the commercially most important species of the NW Mediterranean (Sardà, 1998; Bas, 2006) were selected (Table 2). Conventional agglomerative hierarchical clustering (Zar, 1984) and fuzzy *c*-means clustering (Zadeh, 1965) were used to classify catches (named by the time of day at mid-haul) based on abundances of the selected species. An $n \times p$ matrix was constructed for each survey using swept-area density estimates (ind. km^{-2}) for n species in p hauls.

First, agglomerative hierarchical clustering was used to explore the variation in abundance data using a traditional system based on rigid boundary classifications (Zar, 1984). Density data were normalized by $\log_{10}(x+1)$ transformation to calculate a distance value among catches. The product correlation value for all original levels of matrix similarity and all corresponding similarity values derived from the dendrogram were computed for the Euclidean distance with the unweighted pair group method using arithmetic averages (UPGMA) aggregation method (Lleonart and Roel, 1984). When the UPGMA dendrogram output fits the similarity matrix, its r_c value is 100% (Legendre and Legendre, 1998). In the present study, all r_c values were between 64 and 92%, so the transformations were assumed to represent the original distance matrices reasonably well.

Next, fuzzy *c*-means clustering was used. The methodology allows catches to belong simultaneously to several groups with different membership grades; the membership values range between 0 and 1 (Zadeh, 1965; Zar, 1984). The method applies an iterative algorithm whose aim is to find cluster centres (centroids) that minimize the dissimilarity function:

$$J_m(U, c) = \sum_{i=1}^{c} \sum_{j=1}^{n} u_{ij}^m d_{ij}^2,$$

where U is the fuzzy partition matrix, c the vector of centroids, u_{ij} the degree of membership ($0 \le u_{ij} \le 1$), d_{ij} the Euclidean distance between the ith centroid c_i and the jth (haul) data value, and m ($m > 1$) a weighting exponent determining the degree of fuzziness of the resulting clusters (Bezdek, 1981). The number of hauls (n) varied with season and depth (Table 1). We explored up to $c = 6$ clusters.

The membership matrix (U) was randomly initialized according to the constraint

$$\sum_{i=1}^{c} u_{ij} = 1 \quad \text{for all} j = 1, \ldots, n.$$

Optimal fuzzy partitioning (i.e. to reach a minimum dissimilarity function) is carried out through reiterative optimization of a target equation, with updating of the membership grade value (u_{ij}) to

Table 1. Summary of the trawl surveys.

		Number of hauls				
Sampling dates	**Depth (m)**	**Dawn (06:51–08:49)**	**Daylight (08:50–18:30)**	**Dusk (18:31–20:29)**	**Night (20:30–06:50)**	**Total**
28 September–2 October 1999	430	3	13	5	13	34
2–6 October 1999	110	4	12	4	12	32
		05:21–07:19	**07:20–20:30**	**20:31–22:29**	**22:30–5:20**	
22–26 June 2000	400	4	16	4	7	31
26–30 June 2000	100	3	12	3	7	25

Dawn and dusk ranges encompassed the nominal interval from 1 h before to 1 h after sunrise and sunset.

Table 2. Mean densities (ind. km^{-2}) of targeted commercial species sampled at dawn (DW), by day (D), dusk (Du), and at night (N) on the continental shelf (100–110 m) and upper slope (400–430 m) in October 1999 and June 2000 (see Table 1 for the time ranges).

	Continental shelf								**Upper slope**							
	October 1999				**June 2000**				**October 1999**				**June 2000**			
Species	**Dw**	**D**	**Du**	**N**	**Dw**	**D**	**Du**	**N**	**Dw**	**D**	**Du**	**N**	**Dw**	**D**	**Du**	**N**
Fish																
Citharus linguatula	303	339	834	676	482	444	2 068	1 038	–	–	–	–	–	–	–	–
Eutrigla gurnardus	163	172	119	139	29	111	929	164	–	–	–	–	–	–	–	–
Helicolenus dactylopterus	–	–	–	–	23	208	163	69	400	229	216	189	320	1 059	292	636
Lepidopus caudatus	–	–	–	–	–	–	–	–	19	21	19	34	8	19	10	9
Lepidorhombus boscii	–	–	–	–	–	–	–	–	139	256	130	203	39	62	47	37
Lophius spp.	784	211	975	236	212	89	326	243	154	115	122	119	94	111	115	93
Merluccius merluccius	651	483	235	203	3 165	2 195	1 014	1 578	26	24	63	27	12	21	61	56
Micromesistius poutassou	–	–	–	–	–	–	–	–	41	15	21	27	118	145	150	127
Mullus barbatus	14	19	0	10	209	221	234	145	–	–	–	–	–	–	–	–
Phycis blennoides	279	153	159	133	66	33	113	41	579	999	681	825	1 283	1 766	1 332	1 856
Serranus hepatus	826	519	375	636	794	418	429	425	–	–	–	–	–	–	–	–
Trisopterus minutus	1 776	1 136	781	740	4 112	4 514	2 697	2 930	–	–	–	–	–	–	–	–
Crustaceans																
Liocarcinus depurator	4 168	2 658	9 287	8 978	1 567	824	3 781	2 846	85	54	90	70	39	100	207	89
Macropipus tuberculatus	–	–	–	–	–	–	–	–	0	20	22	32	143	171	194	160
Nephrops norvegicus	55	112	145	178	84	118	109	383	2 484	3 081	413	459	1 465	1 944	760	652
Plesionika martia	–	–	–	–	–	–	–	–	1 546	1 715	1 048	1 375	271	124	872	227
Solenocera membranacea	41	82	3 975	3 160	4 112	151	2 697	2 930	624	862	976	558	876	1 097	846	885
Cephalopods																
Eledone cirrhosa	470	253	96	150	208	–	142	114	–	–	–	–	–	–	–	–
Illex coindetti	42	40	10	14	205	–	438	106	–	–	–	–	–	–	–	–

compute the cluster centroids c_i (Dunn, 1973):

$$u_{ij} = \frac{1}{\sum_{k=1}^{c}((d_{ij})/(d_{kj}))^{2/(m-1)}} c_i = \frac{\sum_{j=1}^{n} u_{ij}^{m} X_j}{\sum_{j=1}^{n} u_{ij}^{m}}.$$

This procedure converges to a local minimum or a load point of J_m.

Summarizing, fuzzy classification requires the following steps: (i) randomly initialize the membership matrix (U), (ii) calculate centroids (c_i), (iii) compute all dissimilarities between all centroids and all datapoints ($J_m(U, c)$), then retain the couples with the smallest dissimilarities, and (iv) compute a new membership matrix $U(u_{ij})$. Repeat steps (i)–(iv) until convergence.

The results of fuzzy clustering are shown as a silhouette according to a given clustering in c clusters (Rousseeuw, 1987). The silhouette shows for each catch the cluster to which it belongs, as well as the neighbour cluster for the catch (i.e. the cluster not containing the catch, for which the average dissimilarity between its observations and a given catch is minimal). The silhouette also shows a width score of the observation. Catches with a silhouette score close to 1 indicate nearly absolute membership for a given group, i.e. not sharing characteristics with another cluster. A silhouette score close to 0 means a catch location between two clusters. Catches with a negative silhouette score indicate misclassification, i.e. no solution found to place the catches into a given cluster.

Finally, to identify the species contributing most to the dissimilarity between clusters of daylight and night groups of catches, a similarity percentage analysis (Clarke, 1993) was applied. The method is based on the Bray–Curtis dissimilarity, d_{rs}, between any pair of clusters r and s, defined as

$$d_{rs} = \sum_{l=1}^{p} d_{rs}(l),$$

indicating the summation over all species p for

$$d_{rs}(l) = 100 \frac{\sum_{l=1}^{p} 2 \min(a_{lr}, a_{ls})}{\sum_{l=1}^{p}(a_{lr} + a_{ls})},$$

where a_{lr} and a_{ls} are the transformed catch ratios of the species l in clusters r and s, and $\min(a_{lr}, a_{ls})$ is the minimum of a_{lr} and a_{ls}.

Results

Continental shelf surveys

On the shelf (100–110 m), both hierarchical and fuzzy clustering methods identified a diel pattern in abundance variation in selected species (Figure 1). Most catches were classified into two or three temporal groups, with only a few exceptions (negative silhouette values in Figure 1). In October, the hierarchical method (Figure 1a) discriminated three groups: a dawn and daylight group of catches (Cluster 1), a dusk and darkness group of catches (Cluster 2), and a group made up of a single catch performed at midnight (Cluster 3). Two catches were performed at dawn but placed in the night Cluster 2 (07:35 and 08:02). Three of the four hauls made around 17:00 were assigned to the night group. A two- and a three-group solution were explored with fuzzy clustering analysis (Figure 1b and c). In the two-group solution (Figure 1b), catches were classified as dawn and morning (Cluster 1) vs. afternoon, dusk, and night (Cluster 2). The catch

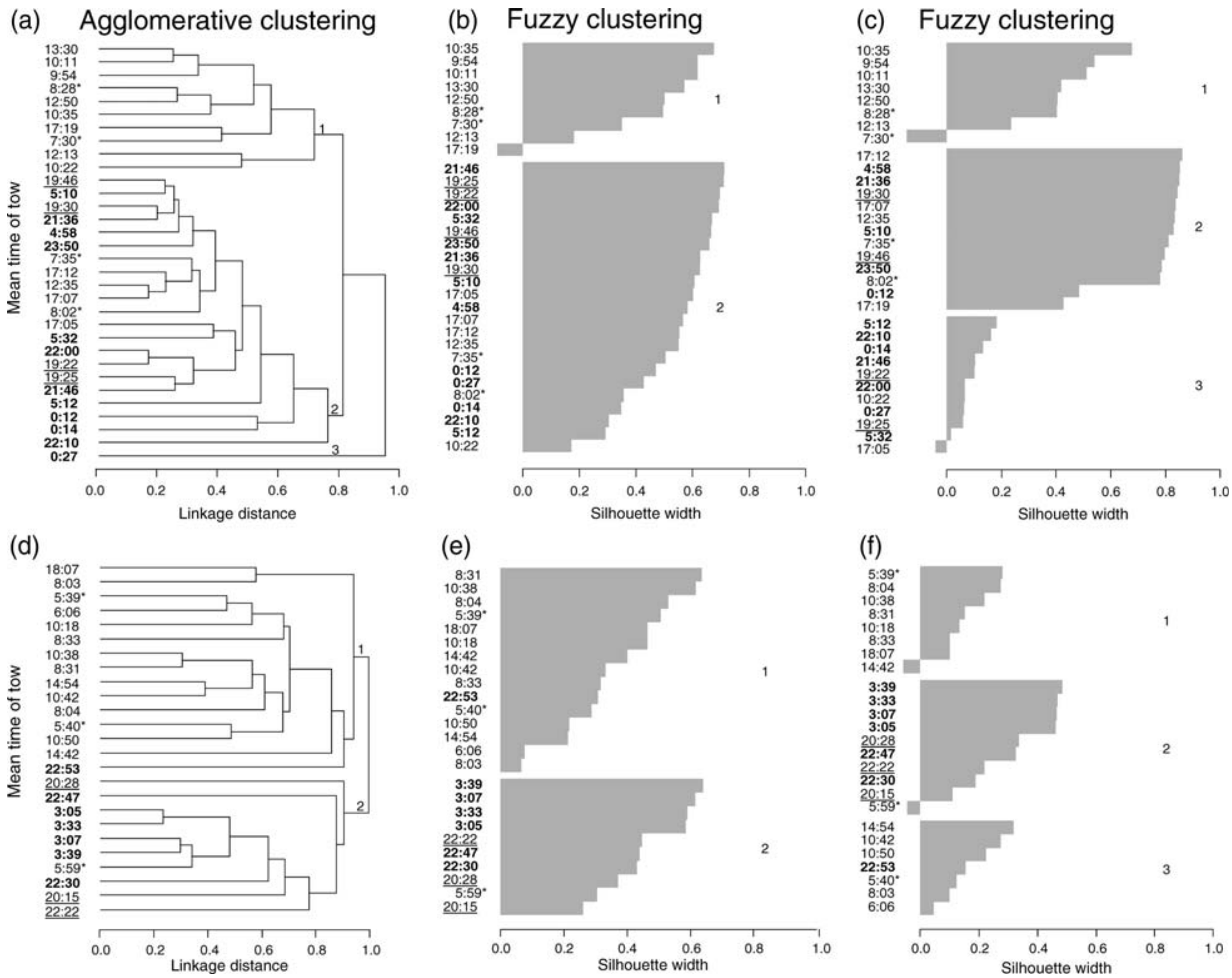

Figure 1. Hierarchical and fuzzy classification of catches undertaken on the continental shelf (100 – 110 m) in (a – c) October and (d – f) June. Catches are identified by the mean time of day of each tow. Night catches are indicated emboldened, dusk catches underlined, dawn catches with an asterisk, and daylight catches unmarked. Different clusters are indicated by ordinal numbers. The scale of agglomerative clustering indicates the degree of similarity among catches: the closer the linkage distance is to 1, the greater the similarity. The fuzzy clustering scale indicates that catches with a silhouette score almost equal to 1 are strongly clustered; a silhouette score close to 0 means that catches were made between two different clusters. A negative silhouette score indicates misclassification.

performed at midnight that was placed on its own in Cluster 3 by the hierarchical clustering method was placed within the Cluster 2 group by the fuzzy method along with other night hauls. A catch performed at 17:19 and allocated to Cluster 1 was misclassified because it had a negative silhouette score. In the three-group solution (Figure 1c), Cluster 1 was basically unchanged and contained all dawn and daylight catches, and the 07:30 catch was misclassified within the daylight group. In contrast, catches at dusk and night were subdivided in two groups (Clusters 2 and 3), both containing samples obtained at various times of day. In Cluster 2, most catches showed nearly absolute, i.e. not fuzzy, night-time memberships (silhouette width close to 1), whereas Cluster 3 was made up of night groups displaying a fuzzier structure with silhouette widths close to 0. The catch performed at noon (12:35) seemed to be atypical because it was placed in the dusk and night (Cluster 2) or night (Cluster 2) groups in the two- and three-group solutions.

In June, the results of both hierarchical (Figure 1d) and fuzzy classifications with two groups (Figure 1e) were identical, producing dawn–daylight and dusk–night clusters. A night-time catch (22:53) was classified within the day group by both methods, however, indicating an atypical species composition. The three-group solution with fuzzy clustering identified a subdivision of the day group into two clusters (Figure 1f). Two morning groups (Clusters 1 and 3) were well-separated from a night group consisting of catches performed between 20:00 and 04:00.

The dissimilarity analysis performed between the clusters produced by the hierarchical and fuzzy (two-group solution) clustering methods showed that *Solenocera membranacea*, a burrowing prawn, and *Nephrops norvegicus*, a burrow dweller, contributed most to the dissimilarity between the day and night catches (between 35 and 41% of the total dissimilarity) in both October and June (Table 3).

Upper slope surveys

The catches on the slope displayed only weak diel periodicity compared with catches on the shelf, because of greater inter-haul variability in species composition (Figure 2). Classification of the catches by both hierarchical and fuzzy analysis methods failed to

Table 3. Contribution (%) of each species to total dissimilarity in the abundances reported between daylight and night clusters of catches on the continental shelf by hierarchical and fuzzy clustering (two-group) analyses.

Species	Day–night dissimilarity (%)			
	Hierarchical clustering		Fuzzy clustering	
Season	October[a]	June[b]	October[c]	June[d]
Mean dissimilarity	17.6	18.5	17.0	18.5
Fish				
Mullus barbatus	10.5	4.8	8.9	4.4
Eutrigla gurnardus	3.8	10.7	3.3	10.0
Serranus hepatus	4.3	5.4	3.4	4.6
Helicolenus dactylopterus	na	8.2	na	8.5
Merluccius merluccius	6.9	4.1	6.9	3.9
Phycis blennoides	3.8	5.6	3.5	5.7
Citharus linguatula	3.9	5.1	4.0	5.2
Lophius spp.	3.4	5.4	3.7	5.5
Trisopterus minutus	3.2	1.6	2.8	1.3
Crustaceans				
Solenocera membranacea	24.2	22.7	27.0	23.1
Nephrops norvegicus	15.1	12.4	14.3	14.2
Liocarcinus depurator	5.2	5.02	5.8	5.5
Cephalopods				
Eledone cirrhosa	6.3	3.2	6.9	3.3
Illex coindetti	9.4	5.8	9.5	4.8

na indicates that no data for *H. dactylopterus* are available in the October survey.
[a]Daylight cluster 1 vs. night cluster 2, as shown in Figure 1a.
[b]Daylight cluster 1 vs. night cluster 2, as shown in Figure 1b.
[c]Daylight cluster 1 vs. night cluster 2, as shown in Figure 1d.
[d]Daylight cluster 1 vs. night cluster 2, as shown in Figure 1e.

identify distinct day and night groups. In October, the hierarchical classification (Figure 2a) identified six clusters of catches: most day catches (12 of 13) were placed in Clusters 1, 3, 4, and 5, whereas most night catches (10 of 13) were placed in Clusters 2 and 6. Most dusk and dawn catches (six of eight) were placed in Clusters 3 and 4. Cluster 2 consisted of a large number of catches (11), nine performed at night between 22:00 and 05:30.

The two-group solution utilizing the fuzzy method (not shown) proved unsuitable for detecting a diel structure in the catches. In the three-group solution (Figure 2b), Cluster 2 comprised solely dawn and daylight catches (six catches). The other catches were distributed between two large clusters comprising mixed day and night catches. Increasing the number of fuzzy clusters from four to six did not provide new information on diel structuring (not shown). A seven-group solution (Figure 2c) led to the identification of diel patterns. Cluster 1 comprised only dusk and night catches (8 catches performed from 21:30 to 05:30), Clusters 3, 6, and 7 mostly included catches (12 of 13) performed from dawn to dusk (the daylight group), and Clusters 2, 4, and 5 showed mixed (mostly day and night) catches.

As in October, in June temporal variations in species composition also showed little diel periodicity (Figure 2d–f). However, hierarchical classification identified eight clusters (Figure 2d): Clusters 1 and 2 comprised daylight catches including one catch at dusk, Cluster 3 included seven catches at dusk and at night plus two in the morning, and Cluster 4 included seven dawn and daylight catches. The other four clusters combined catches performed at any time of the day.

The fuzzy clustering method was applied for two groups (not shown), three groups (Figure 2e), and four groups (Figure 2f). Only the four-group solution identified diel patterns. Clusters 1, 3, and 4 showed a predominantly daylight structure. Cluster 2 (ten catches) contained primarily samples obtained at dusk (four catches) and at night (three of five nocturnal catches). Increasing the number of fuzzy clusters to more than four did not yield biologically meaningful results.

The dissimilarity analysis indicated that the day and night groupings from the hierarchical clustering of catches obtained in October differed with respect to the contributions of the crabs *Macropipus tuberculatus* and *Liocarcinus depurator* along with hake (*Merluccius merluccius*), explaining 44% of the total dissimilarity (Table 4). In June, the shrimp *Plesionika martia* generally contributed most to the dissimilarity among groups.

Discussion

We have shown that temporal variation in the presence and abundance of species within catches, in response to the day–night cycle, influences the species composition of trawl samples primarily in shallow shelf areas (100–110 m) and much less so on the upper deeper slope (400–430 m). Taken together, the results indicated that light is an important environmental factor constraining species availability to trawling on the continental shelf in the Mediterranean Sea and to some degree on the upper slope. Our findings suggest that activity rhythms bias trawl samples when the time-of-day factor is not appropriately taken into account. On the upper slope, the commercial species selected had a fuzzy diel structure, i.e. variations in the species composition by day and night not clear-cut. This indicated that the temporal variation in the upper slope is still somewhat modulated by the cycle of light intensity, but other ecological factors also play a role (Aguzzi *et al.*, 2008a). Hence, fuzzy criteria for catch structure classification are of interest in areas down to the lower boundary of the twilight zone up to ~1000 m, where most of today's extraction fisheries are currently concentrated (Sheppard, 2000; Cartes *et al.*, 2004; Sardà, 2004; Watson and Morato, 2004).

Moving from the shelf to the upper slope, light intensity is reduced by several orders of magnitude (Aguzzi *et al.*, 2003). With an increase in the depth of sampling, species reactivity to day–night cycles is reduced in accord with the reduced perception of fluctuations in light intensity (Aguzzi *et al.*, 2003; Aguzzi and Sardà, 2008). Predation, substratum competition, or other ecological interspecific interactions not considered here potentially influence the diel activity of slope species, masking their response to fluctuations in light intensity (Aguzzi *et al.*, 2008a). Deeper, other recently discovered environmental forces may alter species behaviour with periodicities other than the day–night cycle (Puig *et al.*, 2001). Transient motions of water produced by inertial currents can affect the behaviour of species at a temporal scale of 18 h in the Mediterranean, as can dominant tidal forces in the oceans (reviewed by Aguzzi *et al.*, 2009b). The interaction of these geophysical cycles on the rhythmic behaviour and physiology of species remains to be elucidated. Hence, their effect on temporal variation in species composition as a function of depth is still largely unknown.

In our study, catches rapidly shifted in structure from a dawn–daylight typology to a night typology, starting in early dusk (Tables 2–4). In addition, samples obtained at dawn and dusk did not display any odd transitional structure. These samples were not sufficiently dissimilar in terms of species composition

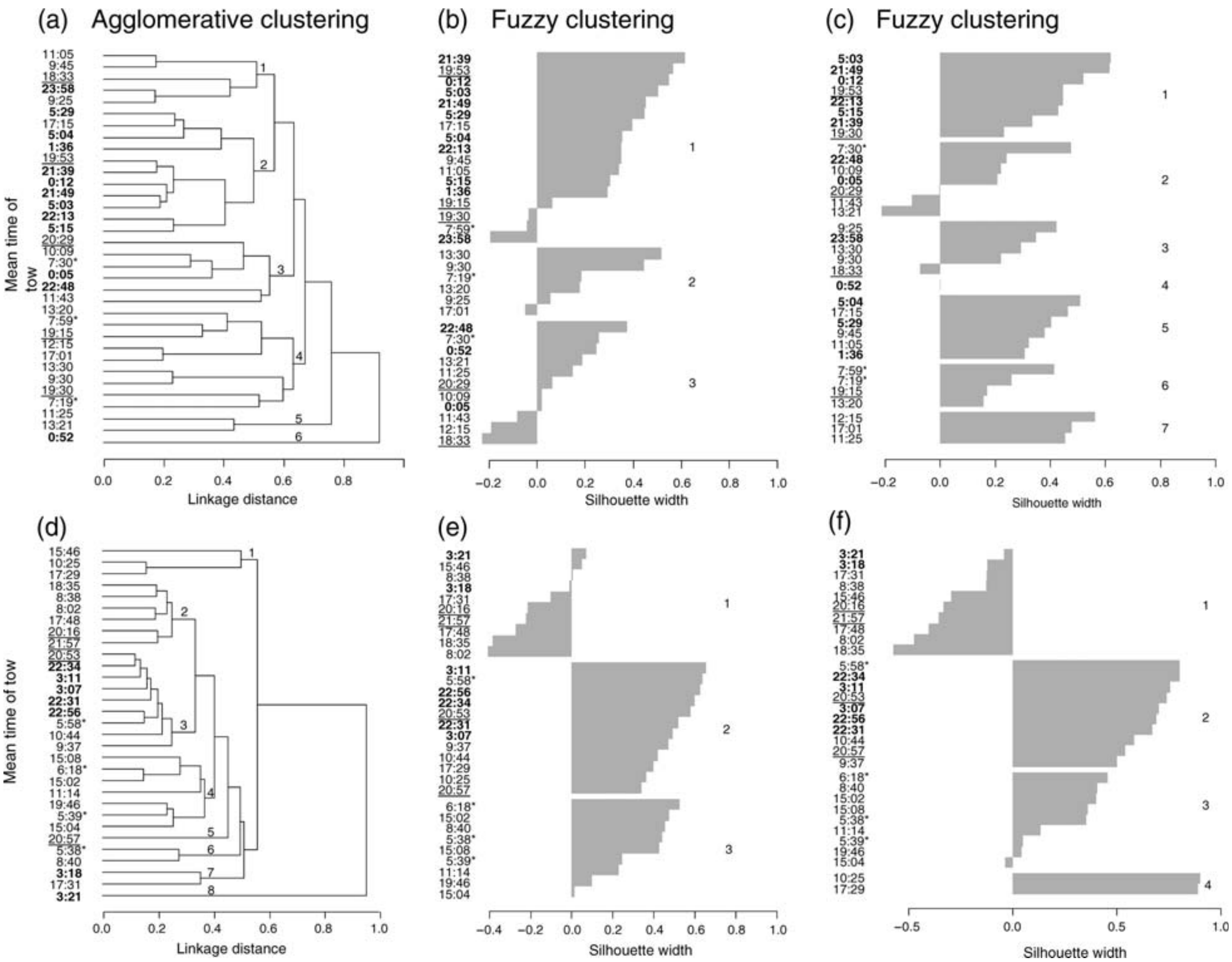

Figure 2. Hierarchical and fuzzy classification of catches carried out on the continental slope (400 – 430 m) in (a – c) October and (d – f) June. Catches are identified by the mean time of day of each tow. Night catches are indicated emboldened, dusk catches underlined, dawn catches with an asterisk, and daylight catches unmarked. The numbers of clusters are indicated. The scale of agglomerative clustering indicates the degree of similarity among catches: the closer the linkage distance is to 1, the greater the similarity. The fuzzy clustering scale indicates that catches with a silhouette score close to 1 are strongly clustered; a silhouette score close to 0 means that the tow lies between two clusters. The tows with a negative silhouette score are probably placed in the wrong cluster (i.e. the fuzzy clustering method is unable to disclose a structural pattern for the catches to be placed in a cluster).

and abundance from those taken at midnight or at midday. Rapid changes in the structure of catches taken in shelf areas are likely attributable to the sudden response of the local community to steeper crepuscular photic transitions (Herring, 2002). In fact, light penetration in the water column depends on the sun's position, and when the sun is directly overhead, a very small percentage of photons is reflected at the sea surface. In contrast, at sunset and sunrise, photon reflection increases and light penetration diminishes. Dusk and dawn variations in light intensity are hence stronger on the shelf, where the angular distribution of light (i.e. transmission) is still asymmetrical in relation to the depth axis. On the slope, the light field is fully symmetrical in relation to depth. As a result, shallow-water species experience steeper light intensity, light colour, and light direction transitions at crepuscular hours than do deeper water species.

The present considerations are supported by the analysis of activity rhythms modulated in response to depth, in species that are present on both the shelf and the upper slope in our samples. For endobenthic decapods, important to the local fishery because of their large biomass, temporal fluctuations in catches vary from a well-defined nocturnal pattern on the shelf to a disrupted pattern on the upper slope (Aguzzi *et al.*, 2007a, b, 2008a, b, c, 2009a). Two opposing forces complicate the temporal analysis in the variation in catch structure (Aguzzi *et al.*, 2008c). First, the light intensity cycle forces emergence into a particular temporal window. Second, the interspecific competition for substratum use forces a shift in activity to avoid predators. This shifts activity to temporal windows other than those favoured by organisms with circadian rhythms controlled by light.

From a methodological perspective, fuzzy classification revealed details on temporal structuring that were not observable in the hierarchical classification results. On the upper slope, fuzzy analysis identified clustering solutions which successfully classified dusk and dawn species assemblages with characteristics borderline between day and night structures. For example, all endobenthic species with a nocturnal emergence habit on the shelf tend to be diurnal on the slope (reviewed by Aguzzi *et al.*, 2009a). The temporal patterning of transitional periods in catch

Table 4. Species contributions (%) to total dissimilarity between daylight and night catches on the continental slope by hierarchical and fuzzy clustering.

Species	Day–night dissimilarity (%)			
	Hierarchical clustering		Fuzzy clustering	
Season	October[a]	June[b]	October[c]	June[d]
Mean dissimilarity	14.7	13.3	15.60	21.0
Fish				
Merluccius merluccius	13.9	10.5	23.2	8.1
Micromesistius poutassou	11.4	4.7	12.2	3.0
Lepidopus caudatus	12.6	8.3	11.4	8.2
Helicolenus dactylopterus	4.8	5.7	4.7	12.2
Lophius spp.	3.7	3.3	4.9	4.1
Lepidorhombus boscii	3.5	8.7	2.5	5.8
Phycis blennoides	2.9	4.3	2.0	3.1
Crustaceans				
Liocarcinus depurator	14.2	8.0	13.3	6.1
Macropipus tuberculatus	15.8	3.9	11.0	4.9
Nephrops norvegicus	9.2	4.2	7.5	10.9
Solenocera membranacea	3.9	3.9	3.0	10.3
Plesionika martia	4.1	34.5	4.3	23.3

[a]Daylight clusters 1, 4, 5 vs. night clusters 2, 6, as shown in Figure 2a.
[b]Daylight clusters 1, 2, 4 vs. night cluster 3, as shown in Figure 2d.
[c]Daylight clusters 3, 6, 7 vs. night cluster 1, as shown in Figure 2c.
[d]Daylight clusters 1, 3, 4 vs. night cluster 2, as shown in Figure 2f.

assemblages of the deeper sampling area is a clear feature in our study, with important implications for scheduling experimental fishing. To achieve a better and more accurate characterization of the two portions of the slope community, i.e. nocturnal and diurnal, field sampling should be centred on midday and midnight, using reliable sample sizes and repeated bottom-trawl surveys (Laevastu and Favorite, 1988).

In October, with 12 h of daylight, shelf catches exhibited a consistently similar structure at sunrise (close to 08:00), mid-afternoon (close to 14:00), late afternoon (at 17:00), and the next sunrise (at 08:00). In June, with increased daylight (from 06:30 to 21:30), there was consistent structuring in catch composition from sunrise (at 06:00) to late afternoon (at 18:00). This demonstrates that seasonal variation in the length of the photoperiod can affect trawl species compositions, rendering the season of sampling an important element of survey planning. On the upper slope, this effect was reflected by the fuzzy cluster analysis, with different numbers of clusters explaining the catches in June and October.

We prefer to use the fuzzy *c*-means clustering method to discern diel patterns in species, stocks, or assemblages showing unclear temporal changes in species composition and abundance. The timing of sampling when catch compositions are analysed to estimate biomass and biodiversity at depths >100 m should be considered carefully. The absence of marked day–night transitions and a consistent reduction in light intensity from the shelf to the slope provokes changes in the rhythmic behaviour of certain species that confine their activity to crepuscular hours.

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