

Microhabitat utilisation by an assemblage of temperate Gobiidae (Pisces: Teleostei)

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ABSTRACT: An assemblage of Gobiidae in Lough Hyne, southwest Ireland, was investigated to assess interspecific and seasonal differences in microhabitat utilisation. Five microhabitat guilds were distinguished using canonical correspondence analysis, comprising 2 semi-hyperbenthic guilds and 3 epibenthic guilds. Differential preferences for each environmental variable measured were examined using Jacobs' version of Ivlev's electivity index. Members of different guilds exhibited differential microhabitat use, whilst members of the same guild exhibited only subtle differences in microhabitat utilisation. Few seasonal variations were observed, with guilds maintaining their separation seasonally.

INTRODUCTION

Analyses of resource utilisation are essential in the study of animal ecology, with successful coexistence relying heavily upon differential resource utilisation. Schoener (1974) deduced that terrestrial animals partition resources along 3 axes – habitat, food, time – in decreasing order. Ross (1986), on the other hand, suggested that in fish communities trophic partitioning was more important than habitat partitioning. However, habitat segregation is thought by many workers to be the most important aspect of resource partitioning in fish communities (Smith & Tyler 1973, Gorman & Karr 1978, Robertson & Lassig 1980, Baker & Ross 1981, Paine et al. 1982). The question of the importance of differential microhabitat use in fish assemblages has led to a wealth of investigations into the effects of environmental variables on fish community structure. However, most studies have been concerned with coral reef (Clarke 1977, Luckhurst & Luckhurst 1978, Bouchon-Navaro 1986, Greenfield & Johnson 1990, Pitts 1991) and freshwater (Werner et al. 1977, Grossman & Freeman 1987, Grossman et al. 1987a, b, Greenberg 1991, Carr 1992) communities. Investigations have demonstrated the importance of substratum type (Luckhurst & Luckhurst 1978), depth (Lindquist 1985, Illich & Kotrschal 1990), and algal abundances (Carr 1989) in particular, in the structuring of fish communities.

In this study, an assemblage of Gobiidae in Lough Hyne, southwest Ireland, was investigated in order to describe interspecific and seasonal differences in microhabitat utilisation.

While temperate Gobiidae have been the focus of several studies (Magnhagen & Wiederholm 1982, Wiederholm 1987, Behrems Hartney 1989, Costello et al. 1990, Wilkins & Myers 1991, Costello 1992), none have considered how coexistence in an assemblage of Gobiidae is maintained seasonally over a range of habitats.

The assemblage in Lough Hyne consisted of: *Gobius couchi* Miller & El-Tawil, *Gobius cruentatus* Gmelin, *Gobius niger* L., *Gobius paganellus* L., *Gobiusculus flavescens* (Fabricius), *Pomatoschistus minutus* (Pallas), *Pomatoschistus pictus* (Malm), and *Thorogobius ephippiatus* (Lowe). Two species of particular interest are *G. couchi*, to date known from only 4 localities (Miller & El-Tawil 1974, Dyrinda & Farnham 1985, Minchin 1988), and *G. cruentatus*, a Lusitanian species at the northernmost point of its distribution in southwest Ireland (Miller 1986).

MATERIAL AND METHODS

Lough Hyne is a sheltered marine lough, the ecology of which has been well documented (Myers et al. 1991); it contains a diversity of habitats, in a location suitable for year-round observation.

Gobies were quantified using 10 sublittoral, 2 m wide continuous belt transects (Baker & Crothers 1987), which were positioned in order to encompass the range of habitats existing within Lough Hyne (Fig. 1). Transects were 40 m long, with the exception of Transect 1 (Fig. 1) which was 50 m long. Each transect was surveyed monthly from January 1989 to December 1990, using SCUBA, during daylight hours. In instances of shoals being observed (*Gobiusculus flavescens*, *Pomatoschistus pictus*), numbers were estimated to the nearest 5.

While environmental data and species densities were obtained per 1 × 2 m, for the purpose of the analyses each transect line was subdivided into discrete microhabitats, which may span more than 1 × 2 m. The microhabitats were defined by the homogeneity of 9 environmental variables, which were: percentage cover of the substratum categories [bedrock, boulders (>0.50 m), rocks (0.10 to 0.49 m), gravel,

muddy shell-gravel, and mud]; depth, measured with a calibrated depth gauge [readings were subsequently converted to depth below the Lough Hyne 'Standard Level' (Bassindale et al. 1948), and average depths were calculated for each microhabitat]; current velocities (m s^{-1}), taken from Bassindale et al. (1957); algal cover, estimated as mean percentage cover of attached macroalgae during the sampling period. An additional variable recorded was the distance of individuals from substratum, fish being recorded as epibenthic or hyperbenthic (>10 cm above the substratum).

In order to determine seasonal differences, data were pooled into winter 1989 (W1; January to March, mean temperature (t) = 10.1 °C, SE ± 0.1), spring 1989 (Sp1; April to June, t = 11.8 °C, SE ± 0.4), summer 1989 (Su1; July to September, t = 15.6 °C, SE ± 0.3), autumn 1989 (A1; October to December, t = 12.2 °C, SE ± 0.9), winter 1990 (W2; January to March, t = 9.1 °C, SE ± 0.1), spring 1990 (Sp2; April to June, t = 11.3 °C, SE ± 0.5), summer 1990 (Su2; July to September, t = 14.7 °C, SE ± 0.2), and autumn 1990 (A2; October to December, t = 12.0 °C, SE ± 0.3).

Data were arranged in 2 matrices: sample by species (50 × 64), containing densities m^{-2} on a seasonal basis; and sample by environmental variable (50 × 10).

In order to test for interspecific differences in microhabitat use, seasonal differences, and environmental variables influencing microhabitat use, matrices were subjected to canonical correspondence analysis (CCA) using the package CANOCO (ter Braak 1987). Species densities were transformed [$\ln(x + 1)$] prior to the analysis. Kruskal-Wallis 1-way analysis of variance tests were applied to the ordination scores in order to determine any intraspecific seasonal variation.

Preferences for each of the environmental variables were evaluated using Jacobs' (1974) modification of Ivlev's electivity index, as in Copp (1992):

$$D = \frac{r - p}{r + p - 2rp}$$

where r = proportion of resource used by a species, and p = proportion of resource available in the environment.

Resource use and availability were determined from measurements of the environmental variables, which were categorised as in Table 1. D is a value

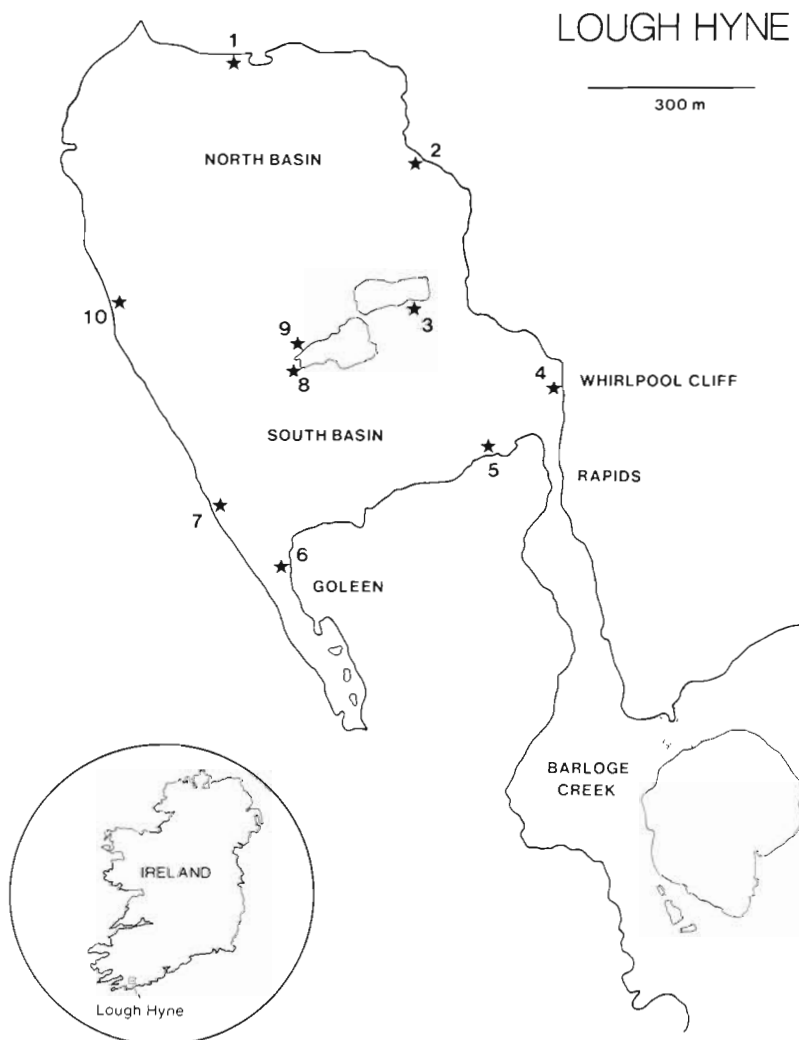


Fig. 1. Lough Hyne, showing position of transect sites

Table 1. Categories of environmental variables for electivity indices (Figs. 4, 5, 6 & 7)

| Variable | Category | | | | | | | | |
|------------------------------|------------|--------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| Mud (%) | Absent | 1-25 | 26-50 | 51-100 | | | | | |
| Rocks (%) | Absent | 1-25 | 26-50 | | | | | | |
| Boulders (%) | Absent | 1-25 | 26-50 | 51-75 | 76-100 | | | | |
| Bedrock (%) | Absent | 1-25 | 26-50 | 51-75 | 76-100 | | | | |
| Muddy shell-gravel (%) | Absent | 1-25 | 26-50 | 51-100 | | | | | |
| Gravel (%) | Absent | 1-25 | 26-100 | | | | | | |
| Algal cover (%) | Absent | 1-33 | 34-66 | 67-100 | | | | | |
| Current (m s ⁻¹) | Absent | 0.01-0.10 | 0.11-0.20 | 0.21-0.35 | | | | | |
| Depth (m) | 0-2.5 | 2.6-5.0 | 5.1-7.5 | 7.6-10.0 | 10.1-12.5 | 12.6-15.0 | 15.1-17.5 | 17.6-20.0 | 20.1-25.0 |
| Distance from substratum | Epibenthic | Hyperbenthic | | | | | | | |

between -1.0 and 1.0 corresponding with total avoidance and total preference for a given category of environmental variable (Jacobs 1974).

RESULTS

Fifty microhabitats were defined, with at least 1 species occurring in each microhabitat.

Fig. 2 presents the CCA ordination diagram for the entire assemblage. Only Axes 1 and 2 are presented, as they cumulatively account for 79.7 % of the total variance. The species-environment correlations of each axis were 0.92 (Axis 1), and 0.77 (Axis 2).

Axis 1 is strongly related to distance from substratum, which results in the epibenthic species clustering separately from the hyperbenthic species. Due to the dominating effect of this environmental variable, a second CCA analysis was carried out on the epibenthic species only, with the hyperbenthic species, *Gobiusculus flavescens* and *Pomatoschistus pictus*, removed from the analysis. Fig. 3 presents the CCA ordination diagram for the epibenthic species only, Axes 1 and 2 cumulatively accounting for 80.3 % of the total variance. The species-environment correlations of each axis were 0.87 (Axis 1) and 0.86 (Axis 2). Axis 1 was principally correlated with boulders and mud cover, whilst Axis 2 was correlated predominantly with depth and algae.

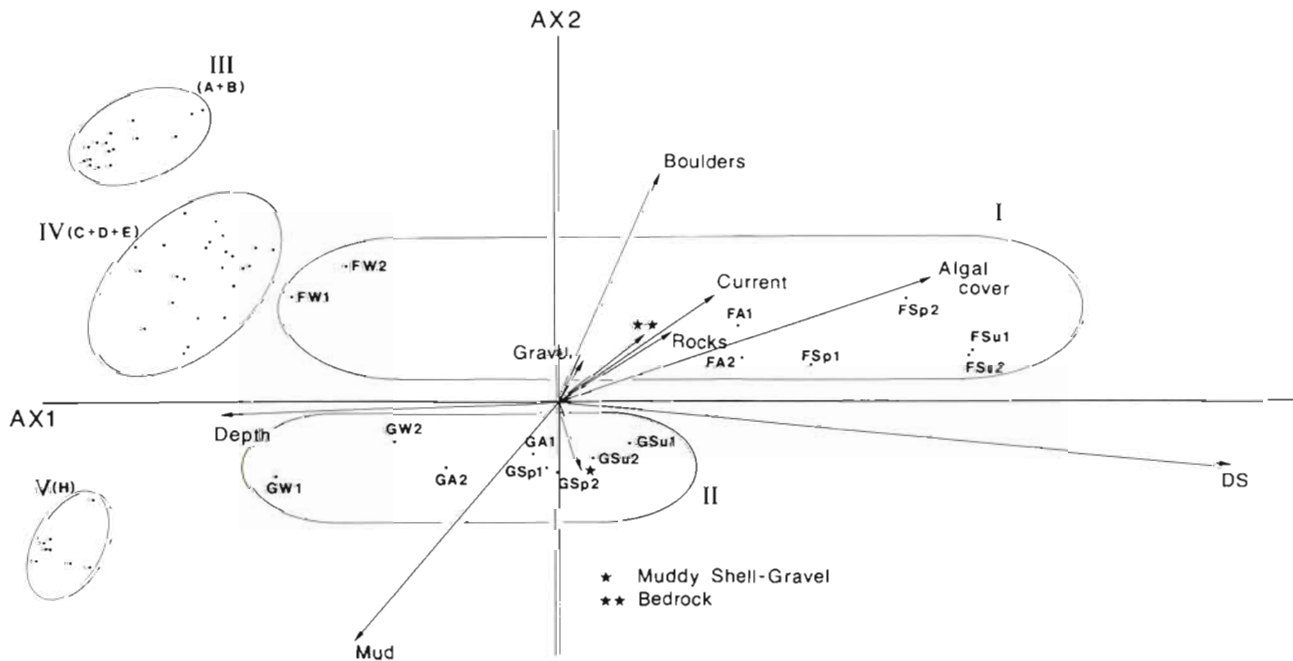


Fig. 2. CCA ordination diagram for all species. A = *Gobius cruentatus*, B = *Thorogobius ephippiatus*, C = *G. paganellus*, D = *G. couchi*, E = *G. niger*, F = *Gobiusculus flavescens*, G = *Pomatoschistus pictus*, H = *P. minutus*, DS = distance from substratum. W, Sp, Su and A followed by '1' or '2' represent seasons (see text for details)

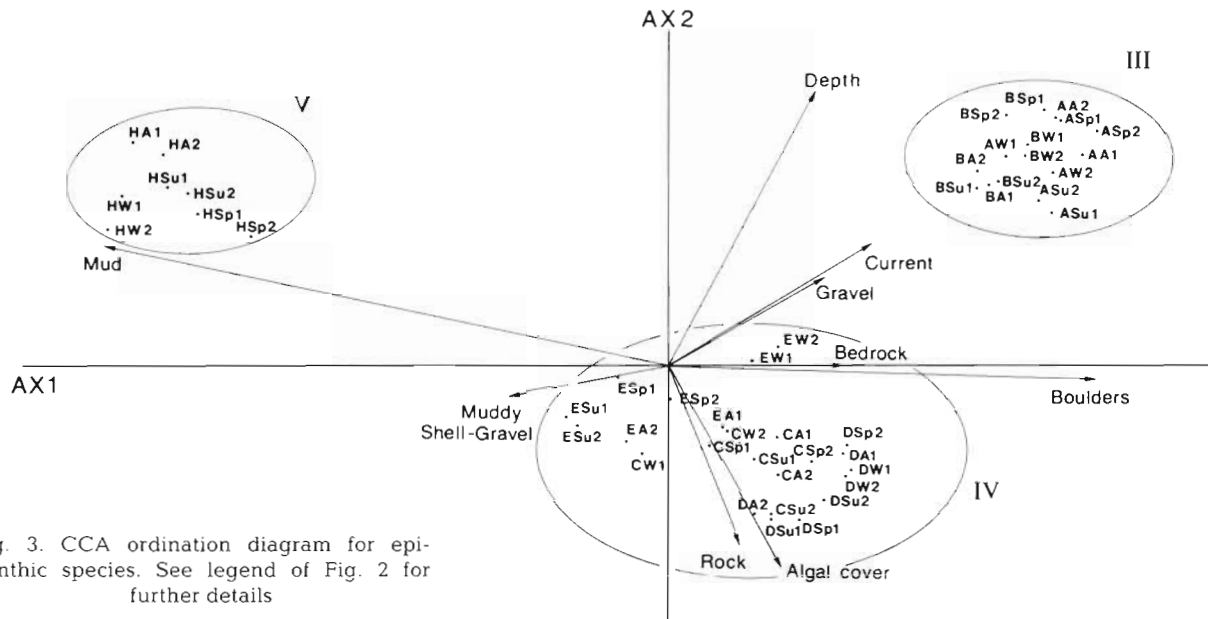


Fig. 3. CCA ordination diagram for epibenthic species. See legend of Fig. 2 for further details

Interspecific differences

Five clusters of species can be identified (Fig. 2). By projecting the relative position of the species points onto the environmental arrows, it is possible to infer which environmental variables have determined the clustering. The clusters can be grouped into an epibenthic group and a semi-hyperbenthic group; *Gobiusculus flavescens* and *Pomatoschistus pictus* make up the semi-hyperbenthic group (clusters I and II), while the remaining species make up the epibenthic group (clusters III, IV, and V) (Fig. 2). It is evident that the presence of algae in a shallow rocky/bouldery area is preferred by *G. flavescens*, particularly in spring, summer, and autumn when this species is largely hyperbenthic (cluster I), while *P. pictus* prefers areas with mud or muddy shell-gravel in slightly deeper water (cluster II) (Fig. 2). Fig. 3 better clarifies the environmental variables that determine the clustering of the epibenthic species.

Cluster III (*Gobius cruentatus* and *Thorogobius ephippiatus*) can be distinguished from the other clusters by its preference for microhabitats containing a high level of boulder cover, in relatively deep water, and with moderate current (Fig. 3).

Cluster IV (*Gobius couchi*, *G. paganellus*, *G. niger*) can be distinguished by its preference for moderate boulder and rock cover, in relatively shallow water, with some degree of algal cover. *G. niger* can be distinguished from the rest of the cluster by its preference for slightly deeper water with a higher degree of mud cover (Fig. 3).

Cluster V (*Pomatoschistus minutus*) is distinguished by a preference for areas consisting of nearly uniform mud cover, with no current, or algal cover (Fig. 3).

The proximity of the species ordination points within clusters III and IV (Figs. 2 & 3) suggests microhabitat co-exploitation; however, within these clusters interspecific differences in microhabitat use can be identified from the electivity indices (Fig. 4).

Clusters I and II differ from the other clusters by being hyperbenthic at certain times, whilst the other clusters are epibenthic at all times (Figs. 2 & 4). The electivity indices for *Gobiusculus flavescens* (cluster I) show this species to be principally hyperbenthic (Fig. 4). A similar trend is seen in *Pomatoschistus pictus* (cluster II), however, this species was less specific in its preference (Fig. 4). Differences between these 2 species exist in substratum preferences, with *G. flavescens* preferring rocky/bouldery areas with high current velocities, whilst *P. pictus* preferred muddy areas with little hard substratum present and no current. *G. flavescens* also differed from *P. pictus* by preferring shallower water, and a high percentage cover of algae, whilst *P. pictus* extended over a larger depth range, and was relatively indifferent to algal cover (Fig. 4).

While there were many similarities in the microhabitat use of *Gobius cruentatus* and *Thorogobius ephippiatus* (cluster III), small differences existed (Fig. 4). The depth preferences of these species were very similar, however *G. cruentatus* extended to slightly shallower depths than *T. ephippiatus*. *G. cruentatus* was indifferent to the presence of rocks, and algal cover, whilst *T. ephippiatus* avoided both of these variables. *T. ephippiatus* preferred areas with low current velocities and relatively high mud cover, whilst *G. cruentatus* preferred areas with moderate to high current velocities, and less mud cover (Fig. 4).



Fig. 4. Electivity indices, pooled over all seasons. See Table 1 for categories of environmental variables, Fig. 2 for abbreviations

Cluster IV is made up of *Gobius paganellus*, *G. couchi*, and *G. niger*. Both *G. paganellus* and *G. couchi* preferred depth ranges from -2.5 to -7.5 m, while *G. niger* extended over a larger depth range. All 3 species preferred low current velocities, although *G. paganellus* was more tolerant of high velocities than *G. couchi* and *G. niger*. All 3 species showed similar patterns in substratum preferences. *G. paganellus* avoided areas with a high percentage cover of mud, while *G. couchi* was indifferent, and *G. niger* preferred areas with up to 50% mud cover. *G. paganellus* was indifferent to the presence of a small amount of gravel, unlike *G. couchi* and *G. niger*, which avoided gravel (Fig. 4).

Pomatoschistus minutus (cluster V) was characterised by its preference for a high percentage cover of mud, with absence of hard substrata, algae and current (Fig. 4).

Seasonal differences

By performing a Kruskal-Wallis 1-way analysis of variance on the CCA axes scores for each species, it was possible to discern any variation along an axis. *Gobiusculus flavescens* and *Pomatoschistus pictus* showed variation along Axis 1 ($p < 0.1$) (Fig. 2), as did the epibenthic species, *Gobius niger* and *P. minutus* ($p < 0.1$) (Fig. 3), whilst *G. cruentatus* and *G. niger* showed variation along Axis 2 ($p < 0.1$) (Fig. 3). Not all variations along an axis were seasonal in nature, thus Figs. 5 to 7 present only those species and environmental variables that exhibited seasonal patterns in variation.

Gobiusculus flavescens exhibited seasonal variation in distance from substratum, being epibenthic in winter, but predominantly hyperbenthic in summer

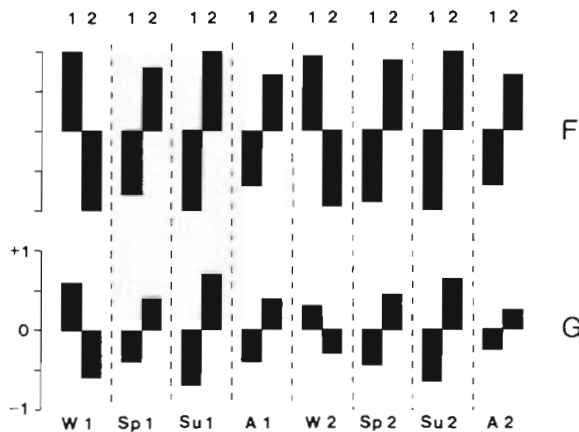


Fig. 5. Electivity indices for seasonal variation in distance from substratum. F = *Gobiusculus flavescens*, G = *Pomatoschistus pictus*. See Table 1 for categories of this environmental variable

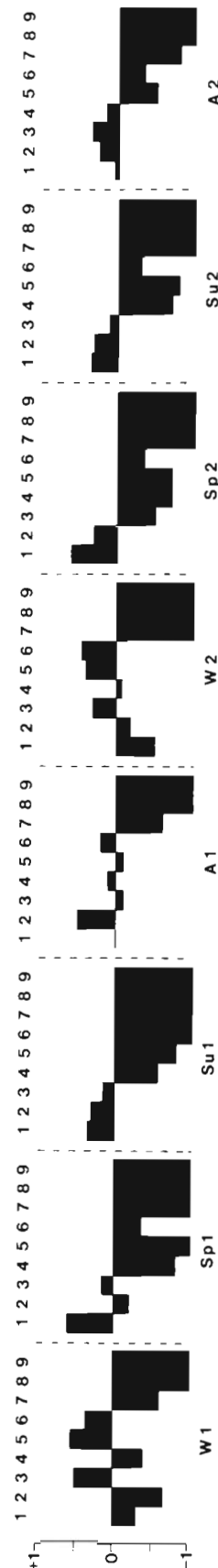


Fig. 6. *Gobiusculus flavescens*. Electivity indices for seasonal variation in depth preference. See Table 1 for categories of this environmental variable

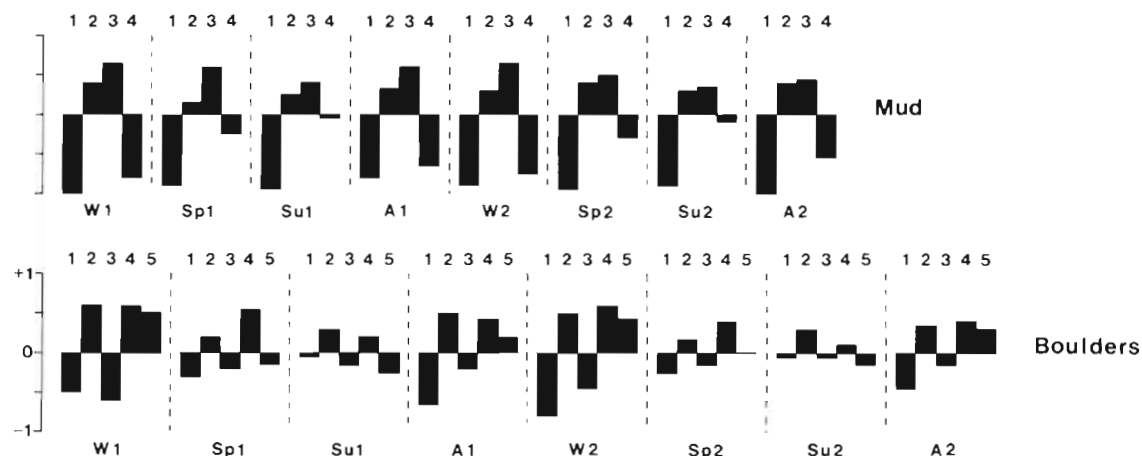


Fig. 7. *Gobius niger*. Electivity indices for seasonal variation in substratum preference. See Table 1 for categories of these environmental variables

(Fig. 5). *G. flavescens* preferred very shallow water in summer, but extended into deeper water in winter (Fig. 6).

Pomatoschistus pictus also showed seasonal variation in distance from substratum. This species was found to be both epibenthic and hyperbenthic throughout the year, however in spring and summer this species tended more towards being hyperbenthic (Fig. 5).

Gobius niger showed seasonal variation in its preferences for mud, and boulder cover. This species preferred a higher percentage of boulder cover in winter than in summer (Fig. 7). It exhibited an inverse trend in preference for mud cover, avoiding areas of high mud cover in winter, and becoming indifferent to areas of high mud cover in spring and summer (Fig. 7).

DISCUSSION

The assemblage of Gobiidae at Lough Hyne exhibited non-random microhabitat utilisation. Two major groups can be recognised – epibenthic, and semi-hyperbenthic – and within these, 5 microhabitat guilds (sensu Hawkins & MacMahon 1989) can be distinguished. The microhabitat guilds can be defined as: (1) a semi-hyperbenthic guild over rocks and boulders in shallow algal-covered areas consisting of *Gobiusculus flavescens*, (2) an epibenthic guild in the same areas, consisting of *Gobius couchi*, *G. paganelus*, and *G. niger*, (3) an epibenthic guild in relatively deep boulder-covered areas, consisting of *G. cruentatus* and *Thorogobius ephippiatus*, (4) a semi-hyperbenthic guild over muddy areas with only a small amount of hard substrata present, consisting of *Pomatoschistus pictus*, and (5) an epibenthic guild on relatively uniform muddy substratum in relatively deep water, which consists of *P. minutus*.

Both *Gobiusculus flavescens* and *Pomatoschistus pictus* occupied both the hyperbenthic and the epibenthic realm. These species frequently occur sympatrically (Iglesias 1981, Collins 1982), and similarities in many aspects of their biology exist (Collins 1981, 1982). Previously in Lough Hyne these species have been recorded shoaling together (Costello 1992). Whilst in summer some mixed shoaling did occur (pers. obs.), these species did exhibit a degree of habitat segregation, with *G. flavescens* preferring shallow rocky algal-covered areas, whilst *P. pictus* preferred areas with less hard substrata, and more mud cover, over a greater depth range. *G. flavescens* was almost always found in association with algae, which Potts & McGuigan (1986), in a study of juvenile *G. flavescens*, attribute to sheltering from predation; similar reasoning can be applied to adult fish (Wheeler 1980). *G. flavescens* exhibited seasonal variation in depth preferences, preferring very shallow waters in summer and spring, and extending deeper in winter. Diminishing algal cover in winter may result in *G. flavescens* being more vulnerable to terrestrial predators such as piscivorous birds, particularly in shallow water (Kruuk et al. 1988), thus *G. flavescens* may move to deeper water as a result of predator pressure. Both *G. flavescens* and *P. pictus* demonstrated seasonal variation in use of the 3 spatial dimensions, with both species occupying the hyperbenthos throughout spring and summer, as well as the epibenthos. Whilst *G. flavescens* became predominantly hyperbenthic in summer, *P. pictus* occurred equally in the epibenthos and the hyperbenthos. In winter, shoaling activity decreased, and both species were mostly found in close association with the substratum, possibly as a result of decreasing activity, associated with decreasing winter temperatures. Small-scale temporal differences in habitat use by *G. flavescens* and *P. pictus*

were also apparent, with both species becoming closely associated with the substratum at night (Costello 1992, authors' pers. obs.), and during the crepuscular periods (authors' pers. obs.), a phenomenon common in some shoaling reef fish (Hobson 1972).

Occupation of the hyperbenthos over the shallow rocky boulder areas by *Gobiusculus flavescens* facilitated coexistence, by vertical spatial segregation, with the epibenthic species, *Gobius couchi*, *G. paganellus*, and *G. niger*. The latter 3 species all showed overlap in most aspects of their habitat utilisation, however differences did exist. *G. couchi* and *G. paganellus* are both documented as inhabiting shallow rocky areas (Wilkins & Myers 1991), whilst *G. niger* has been found in a variety of habitats (Vaas et al. 1975, Nash 1984, Wiederholm 1987, Wilkins & Myers 1991). In this study *G. niger* differed from both *G. couchi* and *G. paganellus* in occupying slightly muddier microhabitats over a larger depth range. Dietary analyses of these 3 species has demonstrated considerable overlap in trophic requirements (McGrath 1974, Miller & El-Tawil 1974, Vaas et al. 1975, Dunne 1978, Chesney & Iglesias 1979), thus competition may occur for food, and microhabitat, particularly between *G. couchi*, and *G. paganellus*.

Gobius niger exhibited seasonal changes in substratum preferences, preferring more open areas in summer than in winter. This may merely be a reflection of decreased activity in winter associated with decreasing temperatures, which results in many benthic species hiding in the substratum (Kotrschal 1983), in this instance boulder crevices. At higher latitudes it has been shown that *G. niger* migrates offshore in winter (Norway; Nash 1984), however, this does not occur at lower latitudes (northwest Spain; Iglesias 1981). The temperature range in Lough Hyne is comparable to that in northwest Spain, which may explain the absence of a winter migration into deeper water by *G. niger*.

Previous studies have remarked on the association of *Gobius cruentatus* and *Thorogobius ephippiatus* with hard substrata (Miller 1969, Dunne 1976, Wilkins & Myers 1991), and the coexistence of these 2 species in Lough Hyne has been noted by Wilkins & Myers (1991). While overlap in microhabitat utilisation was extensive between *G. cruentatus* and *T. ephippiatus*, differences, reflecting differential requirements or competitive exclusion, were apparent in this study. *T. ephippiatus* preferred areas with more mud cover than *G. cruentatus*, whilst *G. cruentatus* was more tolerant of algae than *T. ephippiatus*. This may reflect the different camouflaging properties of these habitats, *T. ephippiatus* and *G. cruentatus* becoming cryptic in areas with mud and algae respectively.

Pomatoschistus minutus occurred in open muddy areas, showing no microhabitat overlap with other

species. *P. minutus* has previously been described as a food generalist obtaining most of its food from the benthos and epibenthos (Hamerlynck et al. 1986), as well as a habitat generalist (Magnhagen & Wiederholm 1982), occupying open areas and algal-covered areas in equal proportion (Wiederholm 1987). This study showed *P. minutus* to actively avoid the macroalgal cover, however, this species was found in the *Audouinella* zone (sensu Kitching et al. 1976) in Lough Hyne (pers. obs.), where the algal mat may have afforded cover and/or food. No seasonal depth migrations were observed for *P. minutus* in this study, although many studies have shown *P. minutus* to perform depth migrations to deeper waters in winter months (Fonds 1971, 1973, Healey 1971, Hesthagen 1975, 1977, 1979).

Jones & Miller (1966) suggest that such migrations occur only when temperatures fall below 5 °C; as temperatures in Lough Hyne rarely fall below 9 °C, this may explain the absence of depth migrations in Lough Hyne. However, Healey (1971) suggests that causation of winter migrations is more complex and cannot be ascribed to temperature alone.

The patterns observed in this assemblage of Gobiidae suggest that habitat segregation is of primary importance, with the 5 microhabitat guilds differentiated on the basis of their distance from substratum, and to a lesser extent by depth, and their differential preferences for mud, boulders, and algal cover. Interactions with non-Gobiidae, differential vulnerability to predation, dietary preferences, morphological and physiological adaptations, and social interactions in addition to historical constraints probably all contribute to segregation of microhabitat guilds (Grossman et al. 1987a, Wiederholm 1987, Copp 1992).

Within microhabitat guilds extensive overlap in microhabitat utilisation existed. Since microhabitat is only a component of the niche, species within microhabitat guilds could segregate along other niche dimensions, however, further studies are required to elucidate whether segregation between microhabitat guild-sharing species is occurring along either trophic or temporal axes.

In summary, 5 guilds were distinguished on the basis of microhabitat utilisation, suggesting the importance of habitat as a niche-segregating mechanism in this assemblage of Gobiidae. Interguild differences were stable both seasonally and annually, suggesting that the existence of the microhabitat guilds may be attributable to evolutionary constraints as well as contemporary competitive interactions. Further investigations are required to determine the relative importance of the various resource dimensions, particularly between microhabitat guild members.

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