Effects of increased habitat complexity on fish assemblages associated with large artificial reef units (French Mediterranean coast)

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Large artificial reef units (LARUs; 158 m³) comprise 38% of 40 000 m³ of artificial reefs deployed in France since 1985. Habitat complexity of one LARU was increased *in situ* in 1991 when 37 m³ of small-sized building materials was placed randomly inside the empty chambers. The fish fauna, before and after added complexity, was compared with the fauna of an unmodified control LARU through 1987–1989 and 1997–1998, respectively, by visual censuses. The experimental LARU showed higher values of all community metrics investigated after treatment: total species richness had become twice as high, mean number of species per census 3 times higher, density 10 times, and biomass 40 times higher. Exceptionally large increases were observed among commercially important species such as sparids. In contrast, few changes were observed at the control unit: species richness had not changed significantly, while density and biomass showed moderate increases by a factor of 2–3, which might be explained by reef maturation. The results confirm the prominent role of habitat complexity in relation to artificial reef design on diversity and abundance of fish assemblages.

Introduction

Of the 40 000 m³ of artificial reefs deployed in France since 1985, Large Artificial Reef Units (LARUs) comprise 38%. LARUs are characterized by a low habitat complexity, having four large and empty chambers and walls with large holes. Previous work has shown that LARU reefs harbour relatively poor fish assemblages, compared with small multimodular reefs (Charbonnel, 1990; Charbonnel *et al.*, 2000). To ascertain the effect of increased habitat complexity of those reefs, small building material was piled up randomly within the empty chambers of one LARU and the fish fauna of two units, one without and one with material added, was evaluated quantitatively through SCUBA surveys. The objective

of this experimental research was to examine if fish abundance and diversity could be enhanced by increased structural reef complexity, and to assess the respective roles of habitat complexity and community maturity (Bohnsack, 1991; Helvey and Smith, 1985), especially in relation to a decrease in void reef space (Hixon and Beets, 1989).

Materials and methods

Reefs studied

A LARU (27 000 kg) consists of nine large concrete slabs, with wide void spaces occupying 158 m³ in volume and providing a surface area of 175 m² for a size of
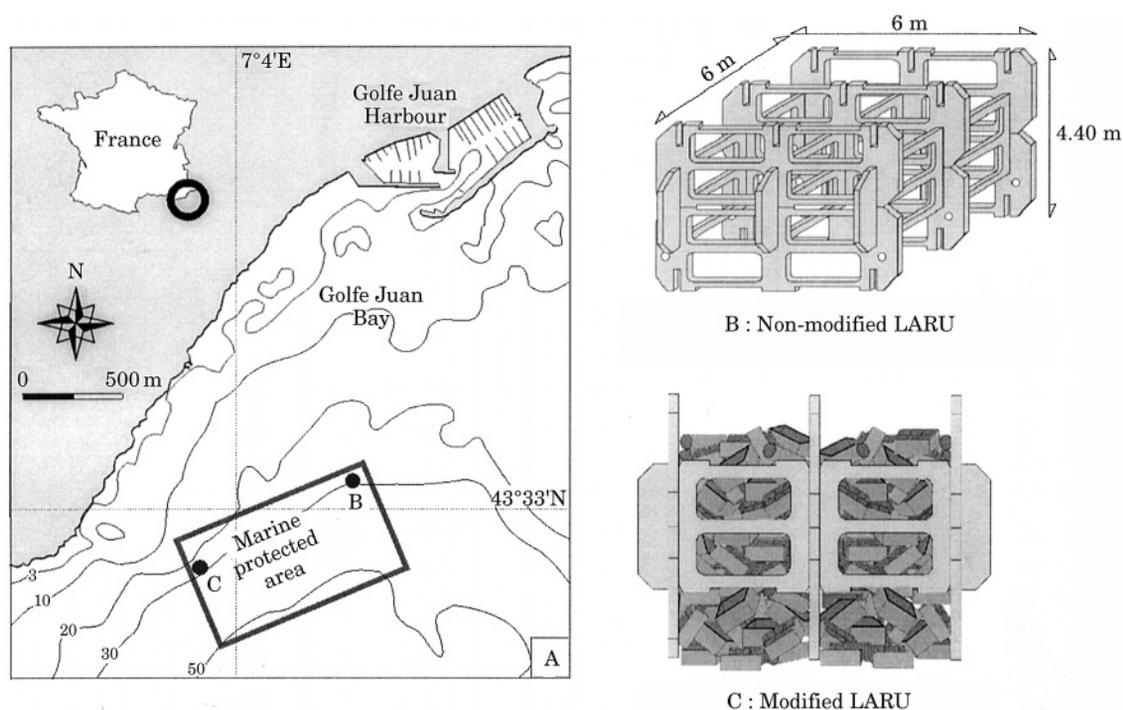
Figure 1. A. Location of Golfe-Juan marine protected area (French Riviera, Alpes-Maritimes). B. control LARU; C: experimental LARU modified by adding small building materials.

$6 \times 6 \times 4.4$ m. The two LARUs studied were deployed in the marine protected area (MPA) of the Golfe-Juan (50 ha with 8000 m^3 of artificial reefs; French Riviera, Figure 1) at 27 m depth on sandy-muddy areas near the lower limit of *Posidonia oceanica* seagrass beds. The control unit was deployed in 1986 in the northern part, near a natural rocky barrier and other artificial structures (3 LARUs and 4 multimodular reefs consisting of chaotic heaps of 36–42 small cubic units of 2 m^3). The experimental unit to be modified was deployed in 1987 in the western part, also near other reefs (2 LARUs and 5 chaotic heaps of 24–36 small cubic units of 2 m^3). In 1991, 37 m^3 of small building materials was piled up randomly inside the empty chambers by divers (468 hollow bricks, 480 breeze blocks, 224 faucet pipes and 40 concrete pipes; size range: 0.023–0.1 m^3 and 0.7–1 m^2). This inner heap of 1212 items offered numerous small interconnected chambers (4110 cavities of various sizes) and an extended surface area (1049 m^2) that was seven times the initial LARU surface. The costs of building materials (excluding diver costs) were about 40% of the original price of one LARU.

Monitoring

Data on fish communities were collected by scuba divers conducting visual censuses (Harmelin-Vivien *et al.*,

1985) specifically adapted for use on artificial reefs (Charbonnel *et al.*, 1997). The two units were monitored between February 1987 and July 1989 (17 censuses) and between October 1997 and July 1998 (20 censuses), thus before and after treatment of the experimental unit. The fish assemblages were characterized in terms of:

- species composition, total and mean species richness (total number of species observed and mean number per census)
- four classes of frequency of occurrence of species: I (75–100%) – permanent species; II (50–75%) – frequent species; III (25–50%) – scarce species; and IV (<25%) – rare species. The relative class composition provides a measure of the temporal variability of the fish assemblage
- density (number of individuals m^{-3} of reef volume)
- biomass (wet weight, in g m^{-3}) calculated from abundance estimates by three size categories (small, medium, and large) using species-specific size-weight relationships (CGPM, 1986).

Differences between frequencies of occurrence were evaluated by means of chi-squared tests. Significant differences between two percentages (p-values) were based on t-tests. Statistical differences among means were evaluated with non-parametric Mann–Whitney Z-tests (Zar, 1997). Most statistical analyses were carried out using StatSoft (1997).

Table 1. Frequency of occurrence (%) of species in relation to treatment, with information on total number of species and mean number before (pre) and after (post) treatment and results of Mann–Whitney tests (*=species with a commercial interest; Vietti *et al.*, 1985).

Family	Species	Control		Experimental	
		Pre	Post	Pre	Post
Sparidae	*Boops boops*	25	0	11	0
	*Dentex dentex**	0	0	0	8
	Diplodus annularis	100	43	45	100
	*Diplodus puntazzo**	0	0	0	38
	*Diplodus sargus**	50	43	22	100
	*Diplodus vulgaris**	63	71	11	85
	*Oblada melanura**	0	0	11	62
	*Pagrus pagrus**	0	14	0	8
	*Spondyliosoma cantharus**	50	14	0	15
Labridae	*Coris julis*	88	100	100	100
	Labrus merula	0	0	0	15
	Labrus viridis	0	0	0	8
	Symphodus cinereus	25	0	22	0
	Symphodus mediterraneus	50	14	56	92
	Symphodus melanocercus	0	0	11	69
	Symphodus tinca	88	57	89	62
Serranidae	*Anthias anthias*	0	0	0	8
	*Epinephelus marginatus**	0	0	0	8
	*Serranus cabrilla**	75	100	100	100
Scorpaenidae	*Scorpaena notata*	13	0	0	62
	Scorpaena porcus	0	0	11	0
	*Scorpaena scrofa**	0	0	11	62
Sciaenidae	*Sciaena umbra**	0	0	0	31
Congridae	*Conger conger**	0	0	0	85
Mullidae	*Mullus surmuletus**	38	43	33	38
Gadidae	*Phycis phycis**	0	0	0	23
Mugilidae	*Mugil* spp.*	0	0	11	0
Rajidae	*Torpedo marmorata**	0	0	0	15
Muraenidae	*Muraena helena**	0	0	0	46
Apogonidae	*Apogon imberbis*	0	0	0	100
Pomacentridae	*Chromis chromis*	75	100	89	100
Centracanthidae	*Spicara maena*	50	43	11	46
	Spicara smaris	0	0	0	8
Blenniidae	*Parablennius gattorugine*	0	0	0	31
	Parablennius rouxii	13	43	0	92
Gobiidae	*Gobius auratus*	0	0	0	23
	Gobius geniporus	0	0	0	100
	Gobius luteus	0	14	11	77
	Thorogobius ephippiatus	0	0	0	8
Tripterygiidae	*Tripterygion delaisi*	0	29	0	77
Total no. of species		15	15	18	36
No. of species census $^{-1}$		8.0 ± 2.0	7.3 ± 2.6	6.6 ± 1.1	18.9 ± 2.5
Mann–Whitney test		Z=0.8; p=0.42		Z= − 3.9; p=0.001	

Results

Fish community composition and species richness

About twice as many species were observed at the experimental LARU after treatment than before treatment, or than at the control unit on both occasions (Table 1). Mean species per census at the experimental unit was significantly larger after treatment than before (by a factor of 3; Z= − 3.9; p=0.001), while differences between the two surveys were not significant for the control.

Overall, 40 species belonging to 17 families were recorded from the two LARUs and the two sampling periods combined. Of these, 36 (90% of the whole species pool) were recorded at the experimental LARU after treatment. Only 17 species were common between the two surveys and 11 among both LARU and surveys (Table 1). Sparids (9 species) and labrids (7) dominated the fish community (40% of the species pool). Almost half of the species (17) are of commercial interest to local fisheries. During the second survey, 4 species were not found again while 19 new species were recorded. Of the
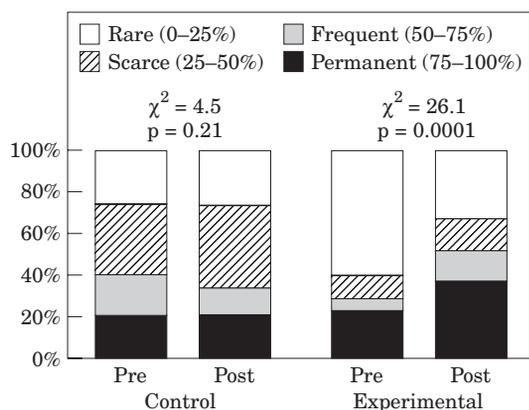
Figure 2. Percentage composition of frequency-of-occurrence classes of the fish species for control and experimental LARU before (pre) and after (post) treatment, with results of chi-squared tests of temporal differences within each unit.

latter, 17 were restricted to the modified LARU (42% of the species pool).

Temporal variability

Changes in the frequency of occurrence after treatment clearly point out the relationship between habitat complexity and temporal variability in the fish community (Figure 2). On the experimental LARU, the contribution of permanent species (36% vs. 22%) and frequent species (14% vs. 6%) increased after treatment, while rare species decreased (33% vs. 61%).

The ''new'' permanent and frequent species (Table 1) included: *Diplodus sargus*, *D. vulgaris*, *Oblada melanura* (sparids with a wide home range), *Scorpaena* spp., *Conger conger*, *Apogon imberbis* (cryptic species dependent on shelter) and some Blenniidae and Gobiidae (benthic species).

On the control, the contribution of permanent and rare species was stable, while the frequency of frequent species decreased (13% vs. 20%) and the frequency of scarce species increased (40% vs. 33%; Figure 2).

Density/biomass

During the first survey, the two LARUs were comparable in terms of fish density, except for Labridae ($Z=2.3$; $p=0.02$; Table 2A). Total density on the experimental LARU showed a highly significant increase (factor 10; $Z=3.9$; $p=0.001$) after treatment, particularly owing to an increase in non-planktivorous species (factor 22). Significant increases were observed throughout the different components of the fish community. The density of planktivorous species decreased (47% vs. 76%) while commercial species had increased in 1998 (from 14% to 39%). Sparidae had become the numerically dominant

family (38% vs. 8%). Cryptic and benthic species appeared only after treatment of the experimental unit.

On the control, a significant increase in total density was also observed over the 10-year period ($Z=2.8$; $p=0.005$) caused particularly by increased abundance of mid-water planktivorous species. Without those, total fish density was not significantly different between the two surveys ($Z=1.2$; $p=0.25$). Like density, estimated total wet weight biomass (with and without planktivorous species) increased significantly on the experimental unit, reaching >1000 g m^{-3} in 1998 (Table 2B; $Z=3.9$, $p=0.001$). However, the factors by which biomass increased (38 and 90, respectively) were much higher than for density, indicating additional effects of an increase of average weight of fish (factor of 4). The contribution of planktivorous species dropped markedly, whereas commercial species reached 95% in 1998. Sparidae clearly dominated the fish community (77%), of which white sea bream (*Diplodus sargus*) was the most important representative (75% of density; 90% of biomass). Cryptic species contributed to 15% of the total biomass, which might be correlated to availability of habitat and/or trophic resources.

The increase in total biomass on the control LARU was not significant ($p=0.09$) and, in contrast to density, the contribution of planktivorous species had decreased (20% vs. 43%).

Discussion

The experimental results indicate that adding a high structural complexity to LARU was an effective way to increasing species richness, abundance and biomass of fish assemblages associated with these extremely simple reef units, and support earlier conclusions about the prominent role that habitat complexity has on the ecological effectiveness of artificial reefs (Shulman, 1984; Helvey and Smith, 1985; Gorham and Alevizon, 1989; Hixon and Beets, 1989; Bohnsack, 1991; Ody and Harmelin, 1994; Sherman *et al*., 2002). The increase in density (10 ×) and biomass in particular (40 ×) was larger than the straightforward increase in surface area related to the piles of building material (7 ×). Excluding planktivorous species, the respective increase factors were even 20 × and 90 × respectively, suggesting that not only increased availability of food plays a role, but that also behavioural aspects are involved. Availability of shelter may be more important, because food resources are generally not limiting (Sale, 1980; Patton *et al*., 1985; Bohnsack, 1991). Also, species may forage directly on artificial reefs, but most species appear to feed on surrounding natural habitat (Harmelin and Bellan-Santini, 1997).

Among the species observed only at the experimental LARU after building material was added, there were

Table 2. Changes in (A) mean density (number of individuals m^{-3} ± s.d.) and (B) mean biomass (g m^{-3} ± s.d.) and the percentage contributions of different components in relation to treatment, before (pre) and after (post) treatment (*significantly different pairs according to Mann–Whitney test; NA: not available).

	Control Pre	Control Post	Experimental Pre	Experimental Post	Control Pre	Control Post	Experimental Pre	Experimental Post
A.			Mean density			Contribution (%)		
Total	0.46 ± 0.24*	1.43 ± 0.90*	0.50 ± 0.27*	5.04 ± 2.53*	100	100	100	100
Non-planktivorous	0.17 ± 0.12	0.42 ± 0.37	0.12 ± 0.06*	2.68 ± 1.85*	37	29	24	53
Planktivorous	0.29 ± 0.22*	1.01 ± 0.65*	0.38 ± 0.25*	2.37 ± 1.34*	63	71	76	47
Commercial	0.17 ± 0.20	0.31 ± 0.34	0.07 ± 0.01*	1.94 ± 1.75*	37	22	14	39
Erratic	0.03 ± 0.00	0	0	0	7	0	0	0
Benthic	0	0.01 ± 0.03	0*	0.08 ± 0.06*	0	1	0	2
Cryptic	0	0.01 ± 0.03	0*	0.56 ± 0.24*	0	1	0	11
Sparidae	0.10 ± 0.12	0.30 ± 0.34	0.04 ± 0.06*	1.91 ± 1.74*	22	21	8	38
Labridae	0.04 ± 0.02*	0.08 ± 0.02*	0.08 ± 0.03*	0.15 ± 0.04*	9	6	16	3
Scorpaenidae	0	0	0*	0.01 ± 0.01*	0	0	0	0.3
B.			Mean biomass			Contribution (%)		
Total	48	78 ± 72	28.1*	1077 ± 817*	100	100	100	100
Non-planktivorous	27	62 ± 64	11.4*	1025 ± 806*	57	79	41	95
Planktivorous	21	16 ± 14	16.6	52 ± 50	43	21	59	5
Commercial	NA	56 ± 62	NA	1004 ± 803	NA	72	NA	93
Erratic	NA	1.0 ± 2.7	0	22.8 ± 75	NA	1	0	2
Benthic	0	0	0	1.0 ± 0.7	0	0.03	0	0.1
Cryptic	0	0	0	157 ± 92	0	0.03	0	15
Sparidae	NA	53 ± 63	NA	828 ± 842	NA	69	NA	77
Labridae	NA	5.4 ± 2.5	NA	9.8 ± 4.2	NA	7	NA	1
Scorpaenidae	0	0	0	3.5 ± 2.9	0	0	0	0.3

two that are protected in Europe according to the Bern and Barcelona Conventions (the grouper (*Epinephelus marginatus*) and the brown meagre (*Sciaena umbra*)) as well as some high-priced target species of fisheries, such as the macrocarnivore sparids (*Dentex dentex* and *Pagrus pagrus*), erratic species that may have used the LARUs as a food resource.

The increased habitat complexity induced significant changes in the entire community structure, particularly in terms of greater species richness (2 × for total richness, 3 × for mean richness). Overall, the community is dominated by sparids and labrids, as is usually the case on Mediterranean artificial reefs (Charbonnel, 1990; Charbonnel *et al.*, 2000) and on rocky substratum (Harmelin, 1987; Ruitton *et al.*, 2000). Among these as well as among other species, a higher proportion was classified as permanent and frequent species based on their frequency of occurrence, suggesting a higher temporal stability of the species assemblage. This may reflect behavioural preferences for a complex environment. The abundance of sparids (a family of prominent commercial interest in the Mediterranean) increased considerably compared to the control, reaching 77% in estimated biomass. In contrast, the difference in biomass of midwater planktivores was not significant, suggesting that these species respond more to the overall structure than to its complexity.

Architecture and module lay-out determine not only the overall performance of the reef in terms of commu- nity metrics but also the identity of species that are able to exploit artificial reefs (Ody and Harmelin, 1994; Charbonnel *et al.*, 2000, 2001). New species appeared after the habitat was modified. Thus, it seems likely that habitat complexity may be manipulated for the benefit of certain target species.

In conclusion, these results stress the importance of choosing an appropriate design before artificial reef deployment. From an ecological point of view, the 95 LARUs (15 010 m^3) that have been deployed in France so far do not appear to be particularly effective because their design does not meet the requirements of the local demersal fish fauna. A reef aimed at maximizing its associated biodiversity should be heterogeneous. The use of a mixture of different kinds of material of different sizes and void spaces in irregular piles facilitates creation of a complex cavity network of small interconnected chambers which appear to provide benefits for many fish species – both predators and prey – that may find features that suit their specific requirements. The positive effects obtained with these multimodular reef types should be taken into account in the design of new artificial reefs that are better suited to the ecological requirements of local fishes.

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