
Artificial fish nurseries can restore certain nursery characteristics in marine urban habitats

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Abstract :

Port areas are subjected to multiple anthropic pressures that directly impact residing marine communities and deprive them of most of their essential ecological functions. Several global projects aim to rehabilitate certain ecosystem functions in port areas, such as a fish nursery function, by installing artificial fish nurseries (AFN). In theory, AFNs increase fish biodiversity and juvenile fish abundance in port areas, but studies on this subject remain scarce. Thus, the present study aimed to examine whether the use of such AFNs could restore part of the nursery function of natural habitats by increasing fish and juvenile abundance, and by decreasing predation intensity compared to bare docks. Two years of monitoring on AFNs showed they hosted 2.1 times more fish than on control docks and up to 2.4 more fish juveniles. Fish community structures were influenced by both treatment (AFN and Control) and year of monitoring. In general, AFNs hosted a greater taxonomic diversity of fish than controls. The predation intensity around these structures was significantly lower in the AFNs than in controls. Part of the definition of a fish nursery was thus verified, indicating that AFNs might be an effective restoration tool. However, we also noted that total fish abundance and Young of the Year (YOY) abundance decreased in controls, possibly due to a concentration effect. Further detailed monitoring is necessary to distinguish between these effects.

Keywords : Ecological restoration, Rehabilitation, Fish, Nursery, Urbanization, Ocean sprawl, Predation

1. Introduction

20 The maritime coastline is a densely populated area. Indeed, 11 of the world's 15 largest cities,
21 half of the cities of more than 100 000 inhabitants, and 40% of the world's population are
22 located within 100km from the seashore (Barragán and de Andrés, 2015; Nazeer et al., 2020;
23 Petrișor et al., 2020). This densification coupled with the intensification of international trade
24 has led to a multiplication of infrastructures and the creation of large-scale port areas (Bugnot
25 et al., 2021; Ducruet and Lee, 2006). This artificialization of the coastline (Fan et al., 2017;
26 Ovejero Campos et al., 2022) in addition to other anthropogenic pressures (Ben Attia et al.,
27 2021) has direct consequences that transform coastal marine habitat characteristics (Airoldi
28 and Beck, 2007; Mooser et al., 2021; Poursanidis et al., 2018; Williams et al., 2022). The
29 prevailing consensus suggests that artificialization is generally associated with a decrease in
30 structural complexity (Bishop et al., 2022; Thrush et al., 2008). However, it is important to
31 acknowledge that this may not always hold true, as it can depend on the specific material and
32 configuration employed in an artificial habitat (Grasselli and Airoldi, 2021). It has been
33 demonstrated that the reduction in complexity in marine environments, leads to a decline in
34 the populations and survival rates of organisms (Brokovich et al., 2006; Fischer et al., 2007).
35 This is linked with a reduction in ecological functions and services (Airoldi and Beck, 2007;
36 Vozzo et al., 2021).

37 This reduction of complexity hampers one essential function of coastal habitats: their role as
38 nurseries for juvenile fish (Courrat et al., 2009; Whitfield and Patrick, 2015). To be considered
39 a nursery, a juvenile fish habitat needs to meet four criteria: (i) it hosts high densities of
40 juveniles, (ii) it provides local food for high juvenile fish growth, (iii) it decreases mortality due
41 to predation, (iv) juveniles settling there actively participate in the renewal of adult populations
42 (Beck et al., 2001). Fish species dependent on coastal nursery areas during their juvenile stage
43 represent 66% of the total landing of the fishery industry and one third of the species surveyed
44 by the ICES (Le Pape et al., 2020; Mora et al., 2008; Seitz et al., 2014). During the life cycle
45 of nursery-dependent fishes, pelagic eggs and larval stages recruit as juveniles to shallow
46 coastal and estuarine nurseries and then move on to adjacent deeper areas as adults (Beck
47 et al., 2001). The survival of juvenile fish after benthic settlement in nurseries is mainly density
48 dependent, and is affected by different biotic and abiotic factors such as food availability and
49 predator abundance (Beck et al., 2001; Belharet et al., 2020; Cheminée et al., 2011; Ford et
50 al., 2016; Ford and Swearer, 2013; Planes et al., 1998; Stewart and Jones, 2001). The surface
51 area of nurseries is therefore essential for the maintenance of these populations (Le Pape and
52 Bonhommeau, 2015). However, the loss of nursery habitats due to urbanization has led to the
53 over-mortality of juveniles, allowing only very limited success for recruitment to adult
54 populations (Bouchoucha et al., 2016; Cheminée et al., 2017; Harmelin-Vivien et al., 1995).

55 This impairs the renewal of adult nursery-dependent fish populations (Limiting Recruitment
56 Hypothesis; Doherty, 1991).

57 Ecological rehabilitation operations have been considered to counteract the loss of ecosystem
58 function due to urbanization. The principle of rehabilitation operations in port areas is broadly
59 invariant and is based on eco-engineering (Airoldi et al., 2021; Dafforn et al., 2015; Strain et
60 al., 2018). Flat, steep and smooth urban structures are considered inadequate for providing
61 habitats for marine biodiversity, so artificial modules are added to them to increase their
62 structural complexity (Bishop et al., 2022; Bradford et al., 2020). This approach is used to
63 ensure marine benthic diversity (Bishop et al., 2022; Strain et al., 2020) as well as to restore
64 the fish nursery function of urban habitats (Astruch et al., 2017; Bouchoucha et al., 2016;
65 Lapinski et al., 2017; Patranella et al., 2017; Ushiyama et al., 2019).

66 Previous studies have shown the ability of artificial fish nurseries (AFN) installed on port
67 structures, docks or pontoons, to host important densities of juvenile fish (Bouchoucha et al.,
68 2016; Mercader et al., 2017). However, studies focusing on multiple species and with robust
69 designs remain rare (Firth et al., 2020). In particular, many studies focusing on juvenile fishes
70 have been limited to measuring the abundance of individuals observed on AFNs (Astruch et
71 al., 2017; Bouchoucha et al., 2016; Mercader et al., 2017; Patranella et al., 2017), neglecting
72 to consider the crucial aspect of predation, which is one of the fundamental functions of fish
73 nurseries (Beck et al., 2001).

74 The present study aimed to document the effect of AFNs installed on docks to increase their
75 structural complexity. We tested the hypothesis of whether the addition of these AFNs
76 increases the abundance and species diversity of fish and fish juveniles compared to bare
77 docks, and whether they provide shelter from predation by reducing predation intensity. To do
78 so, we monitored fish population, particularly juveniles, during a two-year campaign, on docks
79 equipped with AFNs and on bare docks in a Mediterranean port. We also estimated pelagic
80 predation intensity in the same areas. Our study is aimed at improving knowledge of the
81 benefits of using AFNs for rehabilitating the nursery function in ports.

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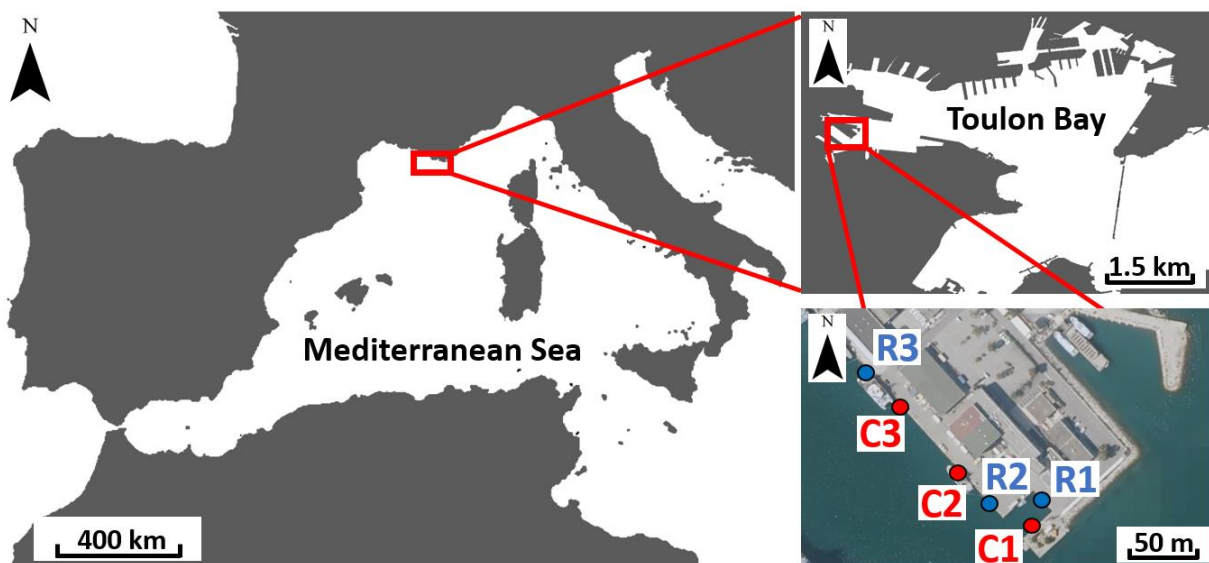
83 **2. Material and Methods**

84 **2.1. Study site**

85 The study was carried out on the docks of the industrial port of La Seyne-sur-Mer near Toulon
86 (43.105960°N; 5.884599°E; Fig. 1). The Toulon Bay encompasses 9.8 km² of artificial habitats
87 (military port, commercial port and 6 marinas), isolated from the open Mediterranean Sea by a
88 1.2 km long breakwater. The city's industrial and military history make it one of the most
89 polluted marine areas in Europe in terms of metallic trace elements (e.g. Cu, Pb, Hg) and

90 persistent organic pollutants (PAH, PCB; Pougnet et al., 2014; Tessier et al., 2011; Wafo et
91 al., 2016). Since 2019, several AFNs have been installed in certain ports of Toulon bay in the
92 framework of an experimental assay to rehabilitate part of the fish nursery function lost in these
93 areas (Bouchoucha et al., 2018a, 2018b, 2016; Gauff et al., 2023). Our monitoring focused on
94 such structures, installed in June 2020 at La Seyne-sur-Mer. The docks studied were about
95 300 m long, up to 6 m deep, and designed to accommodate part of the French oceanographic
96 fleet. Three 50 m² areas separated by at least 50 m (sites, Figure 1) were equipped with 2 x 5 m
97 long strands covered with 30 cm long flexible polypropylene fiber rods. These AFNs are
98 designed to mimic seagrass meadows (Figure 2). On each site, the sub-sets are arranged one
99 under another at 50 cm intervals between 20 cm and 5.20 m depth (Figure 2 and 3). Fish
100 diversity and abundance were assessed at least twice a month for a period of 24 months from
101 June 2020 to May 2022. For each replicate site, fish abundance was recorded on an AFN as
102 well as on a control area consisting of a 10 x 5 m (50 m²) vertical surface of bare dock. The
103 distance between the AFN and the control was at least 20 m.

104



105

106 *Figure 1: Map of the study site (La Seyne-sur-Mer, Toulon Bay, French Mediterranean). The*
107 *position of the artificial fish nurseries studied (Blue; R) and control dock (Red; C) is indicated.*



108

Figure 2: Picture of A.: Artificial fish nursery installed on the docks and B. control dock (photo credit, Ifremer O. Dugornay).

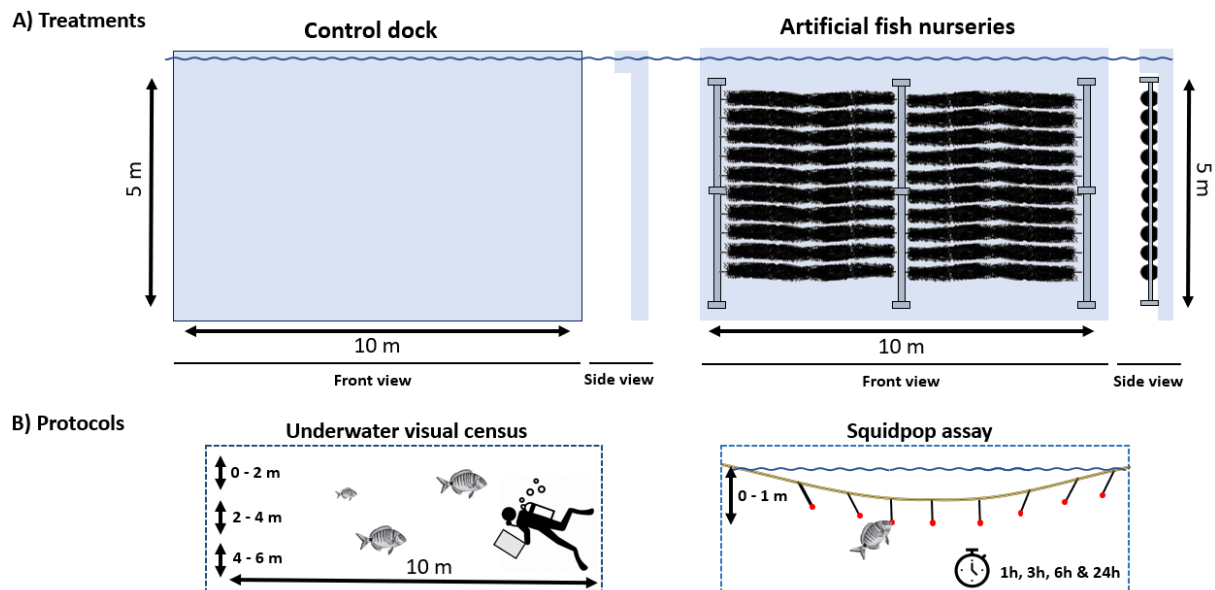
109

2.2. Fish abundance and diversity monitoring

110

Abundances for all fish species were estimated by underwater visual census using slow-swimming underwater transects (Cheminée et al., 2017; Harmelin-Vivien et al., 1995). Due to generally poor visibility conditions, the survey area was covered in three passes at three different depths (0 to 2 m, 2 to 4 m, 4 to 6 m), starting from the top of the AFN or dock. Each transect (replicate) corresponds to the sum of abundance of fish species observed during these three passes. The space between the AFN and the pier was also investigated. During the monitoring, all the individuals identified to the lowest possible taxonomic level (species) were counted and their sizes were estimated (total length, $TL \pm 5$ mm) by the same diver. In order to distinguish between juvenile and adult individuals of each species, the Young of the Year (YOY) were identified *a posteriori* based on the size of the individuals compared to demographic data from Félix-Hackradt et al. (2013). In the absence of data on the YOY size of certain species, the size of the YOYs was considered to be 1/3 of the average observation size of adults, collected from FishBase (Froese and Pauly, 2022). The survey was carried out between 10:00 and 16:00 h, and poor visibility conditions were consistently avoided.

123



124
125 *Figure 3: Illustration of the A) Treatments (Control & Artificial Fish Nurseries) and B) Protocols*
126 *of experiments (Underwater visual census and Squidpop assay).*

127 **2.3. Identification of potential predators and predation intensity**

128 To evaluate predation intensity among sites equipped with AFNs and control areas, a Squidpop
129 feeding assay was used to directly measure predation intensity. The Squidpop assay was
130 developed to measure fish predation intensity in different environments and consists of
131 standardized squid baits attached to fiberglass stakes (Duffy et al., 2015). This assay has been
132 used in various environments, including artificial habitats (Duffy et al., 2015; Gauff et al., 2022;
133 Kough and Belak, 2022; Rodemann and Brandl, 2017). The choice of squid as bait is
134 associated with its mechanical qualities (Gauff et al., 2022). Here, we used a modified version
135 of the Squidpop protocol: for each of the three replication sites, 11 baits positioned 1 m apart
136 were suspended on a rope between the surface and one meter deep for 24h, close to the AFN
137 areas and at the control areas (Figure 3). This was repeated thrice (6th and 20th June, 7th July
138 2022), resulting in a total of 9 replicates for each treatment (AFN & Control). To provide higher
139 resolution on bait consumption dynamics, the remaining baits were counted 1 h, 3 h, 6 h and
140 24 h after deployment, making it possible to carry out survival analysis (Gauff et al., 2022,
141 2018). The survival rate is considered to provide a *proxy* of predation intensity (Gauff et al.,
142 2022).

143 **2.4. Statistical analysis**

144 All statistical analysis were performed using 'R' (version 4.2.2; R Core Team, 2022).

145 *2.4.1. Fish abundance analysis*

146 Mean density and associated standard error were expressed in individuals per 100 m². We
147 tested the influence of the treatment (fixed, two levels: AFN and Control), the year of monitoring

148 (fixed, two levels: Year 1 and Year 2), and their interaction on the observed density of fish and
149 YOYs. Site (three levels: Site 1, Site 2, Site 3) was considered as a random factor. The density
150 data did not follow a normal distribution. We thus fitted a generalized linear model following a
151 negative binomial distribution (`glmer.nb`) from the 'lme4' R package (version 1.1-31; Bolker,
152 2022). The Goodness Of Fit (GOF) of the model was checked using the 'plotresid' function
153 from the 'RVAidememoire' package (version 0.9-81-2; Hervé, 2022) which allowed us to
154 graphically verify the model's residuals and then test dispersion using the 'dispersion_glmer'
155 function from the 'blmeco' package (version 1.4; Korner-Nievergelt, 2019). When the
156 interaction term was significant in the generalized model, we performed a post hoc comparison
157 of density means using a 'Tukey contrast' multiple comparison test using the 'glht' function
158 from the 'multcomp' package (version 1.4-20; Hothorn, 2022). During the multiple comparisons
159 tests, the p-values were adjusted by the Benjamini and Hochberg (BH) correction (Benjamini
160 and Hochberg, 1995).

161 *2.4.2. Community analysis*

162 The effect of treatment (fixed, two levels: AFN and Control), year of monitoring (fixed, two
163 levels: Year 1 and Year 2) and their interaction on species richness was assessed with a
164 generalized linear model with negative binomial distribution (Bolker, 2022). Subsequent
165 analysis followed the workflow described for fish abundances (see §2.4.1.). Community
166 structure analyses were conducted using Bray-Curtis dissimilarity matrices, obtained with the
167 'vegdist' function from the 'vegan' package (version 2.6-4; Oksanen, 2022). The specific
168 communities during monitoring were visualized by plotting a Non-metric Multidimensional
169 Scaling (NMDS) created using the 'metaMDS' function from the 'vegan' package (version 2.6-
170 4; Oksanen, 2022). A PERMANOVA (10^4 permutations; Anderson, 2001) was performed to
171 test the influence of the treatment, the year of monitoring, and their interaction on the observed
172 community of all fish and YOYs. The permutation structure was nested within sites. Post hoc
173 comparison was performed with a pairwise PERMANOVA (10^4 permutations) from the
174 'pairwiseAdonis' package (version 0.4; Martinez Arbizu, 2020). The p-values were adjusted by
175 a Benjamini and Hochberg correction (Benjamini and Hochberg, 1995).

176 To assess whether certain species were representative of one treatment, we carried out a
177 multipattern analysis (10^4 permutations) from the 'indicspecies' package (version 1.7.12; De
178 Cáceres, 2022). The test was set up to perform comparisons within the two main factors
179 (treatment and year) and their four interaction terms.

180 *2.4.3. Predation intensity analysis*

181 The Squidpop assays were analyzed *via* survival analysis (Pyke and Thompson, 1986) using
182 the 'survival' package (version 3.4-0, Therneau, 2023). The time at which the absence of an

183 individual bait was recorded was considered its survival time (Gauff et al., 2018). Kaplan-Meier
184 curves of bait survival were computed for each treatment (George et al., 2014; Rich et al.,
185 2010). Survival rates in different treatments were compared with a nested Cox model from the
186 'NestedCohort' package (version 1.1-3; A Katki, 2013) in order to test whether treatments
187 differed in predation intensity (Pyke and Thompson, 1986; Rich et al., 2010). In this model
188 individual baits were nested within site and date.

189 **3. Results**

190 During the first year, 52 surveys were carried out on AFNs and 51 on controls. Due to
191 unexpected adverse environmental conditions (e.g., occasional days with poor underwater
192 visibility) or logistic constraints (e.g., the presence of oceanographic vessels at dock, COVID
193 lockdowns, etc.), the sampling effort was lower during the second year, with 29 censuses
194 carried out on AFNs and 28 on controls. However, this did not prevent accurate investigation
195 of AFNs, as all of the three sites were fully surveyed at least twice per month over the whole
196 duration of the study.

197 **3.1. Fish abundance monitoring**

198 Over the surveyed time period a total of 3062 fish of 43 species were identified. The majority
199 of the individuals (70%) were found in the AFNs, together with higher species richness (42
200 species on AFN compared to 29 on control; Table 1). Treatment significantly interacted with
201 the Year of study for both models (GLMER.nb, z.value = -3.61, $p < 0.001$ and z.value = -2.73,
202 $p = 0.006$; Tab. 2). During the first year of monitoring, fish density on AFNs (42.6 ± 4.4 ind.100
203 m^{-2} ; all life stages combined) was significantly higher than on controls (28.2 ± 5.2 ind.100 m^{-2} ;
204 GLHT, z.value = -2.365, $p = 0.018$; Fig. 4, Tab. 2). This trend continued in the second year
205 with a significantly higher fish density on AFNs (70.6 ± 8.4 ind.100 m^{-2}) than on control (17 ± 3
206 ind.100 m^{-2} ; GLHT, z.value = -6.227, $p < 0.001$; Tab. 2). Concerning YOYs, 817 individuals
207 were recorded, of which 72% were on AFNs. No significant difference in density was found for
208 YOYs (GLHT, z.value = -1.811, $p = 0.098$) between AFNs (16 ± 2.8 ind.100 m^{-2}) and controls
209 (9.3 ± 3 ind.100 m^{-2}) in the first year (Figure 3). However, in the second year higher densities
210 were observed on AFNs (17.3 ± 5.8 ind.100 m^{-2}) compared to control (2.4 ± 1.2 ind.100 m^{-2} ;
211 GLHT, z.value = -4.515, $p < 0.001$; Tab. 2). A slight overall increase of fish densities but not
212 YOY densities could be noted between the two years surveyed (main effect; GLMER.nb,
213 z.value = 2.682, $p = 0.008$). Total fish densities on AFN increased between Year 1 and Year 2
214 (GLHT, z.value = 2.674, $p = 0.011$). On the contrary, total fish densities on controls decreased
215 between Year 1 and Year 2. Concerning YOYs, their density on AFNs did not differ between
216 the two years (GLHT, z.value = 0.22, $p = 0.82$; Tab. 2). This is not the case for control, where

217 a significant decrease in the density of YOYs between Year 1 and Year 2 could be noted
 218 (GLHT, z.value = -3.39, p < 0.002; Fig. 4, Tab. 2).

Family	Species	Year.1		Year.2		Total (YOY)
		AFN Tot. (YOY)	Control Tot. (YOY)	AFN Tot. (YOY)	Control Tot. (YOY)	
Atherinidae	<i>Atherina sp.</i>	73 (0)		33 (33)		106 (33)
Blenniidae	<i>Microlipophrys canevae</i>		3 (0)		22 (0)	25 (0)
	<i>Parablennius gattorugine</i>		2 (0)			2 (0)
	<i>Parablennius sanguinolentus</i>	1 (0)				1 (0)
	<i>Salaria pavo</i>	1 (0)		1 (0)	1 (0)	3 (0)
Carangidae	<i>Trachurus mediterraneus</i>	68 (68)	30 (30)			98 (98)
	<i>Trachurus sp.</i>		50 (50)			50 (50)
Gobiidae	<i>Aphia minuta</i>		94 (0)			94 (0)
	<i>Gobius cobitis</i>		3 (0)	1 (0)	3 (0)	7 (0)
	<i>Gobius cruentatus</i>	44 (1)	16 (0)	16 (0)	18 (0)	94 (1)
	<i>Gobius geniporus</i>	19 (2)	27 (2)	6 (0)	13 (0)	65 (4)
	<i>Gobius niger</i>	11 (4)	13 (0)	13 (1)	6 (1)	43 (6)
	<i>Gobius paganellus</i>		5 (0)	1 (0)	2 (0)	8 (0)
	<i>Gobius xanthocephalus</i>	7 (0)	29 (0)	38 (8)	31 (0)	105 (8)
	<i>Pomatoschistus quagga</i>			1 (0)		1 (0)
	<i>Pseudaphya ferreri</i>			2 (0)	10 (0)	12 (0)
	Labridae	<i>Labrus merula</i>	5 (1)		8 (1)	
<i>Symphodus cinereus</i>		48 (2)	39 (0)	24 (0)	9 (0)	120 (2)
<i>Symphodus mediterraneus</i>		1 (0)		1 (0)		2 (0)
<i>Symphodus melanocercus</i>				1 (0)		1 (0)
<i>Symphodus melops</i>		2 (0)				2 (0)
<i>Symphodus ocellatus</i>		5 (0)		9 (1)	2 (0)	16 (1)
<i>Symphodus roissali</i>		3 (0)	7 (0)	6 (2)		16 (2)
<i>Symphodus rostratus</i>		6 (0)	1 (0)			7 (0)
	<i>Symphodus tinca</i>	156 (16)	83 (23)	100 (2)	14 (0)	353 (41)
Moronidae	<i>Dicentrarchus labrax</i>	3 (0)		9 (3)		12 (3)
Mugilidae	<i>Mugil cephalus</i>			2 (0)		2 (0)
	<i>Mullus barbatus</i>	13 (10)	1 (1)	2 (0)		16 (11)
	<i>Mullus surmuletus</i>	57 (28)	30 (29)	20 (11)	5 (3)	112 (71)
Scorpaenidae	<i>Scorpaena scrofa</i>	1 (0)				1 (0)
	<i>Scorpanena porcus</i>	1 (0)				1 (0)
Serranidae	<i>Serranus scriba</i>	2 (0)				2 (0)
Sparidae	<i>Diplodus annularis</i>	79 (32)	18 (7)	106 (58)	6 (2)	209 (99)
	<i>Diplodus puntazzo</i>	22 (18)	4 (1)	7 (6)	2 (0)	35 (25)
	<i>Diplodus sargus</i>	215 (60)	61 (25)	349 (21)	9 (0)	634 (106)
	<i>Diplodus vulgaris</i>	101 (45)	63 (30)	86 (17)	35 (8)	285 (100)
	<i>Pagellus sp.</i>			4 (4)	8 (0)	12 (4)
	<i>Sarpa salpa</i>	125 (86)	84 (0)	149 (48)	11 (0)	369 (134)
	<i>Sparus aurata</i>	2 (0)		2 (0)		4 (0)
	<i>Spicara sp.</i>	2 (2)			13 (13)	15 (15)
	<i>Spondylisoma cantharus</i>	1 (1)				1 (1)
Tripterygiidae	<i>Tripterygion delaisi</i>	17 (0)	21 (0)	20 (0)	17 (0)	75 (0)
	<i>Tripterygion tripteronotum</i>	15 (0)	11 (0)	6 (0)	1 (0)	33 (0)
Total		1106 (376)	695 (198)	1023 (216)	238 (27)	3062 (817)
number of species (YOY)		32 (16)	24 (10)	29 (15)	22 (5)	43 (23)

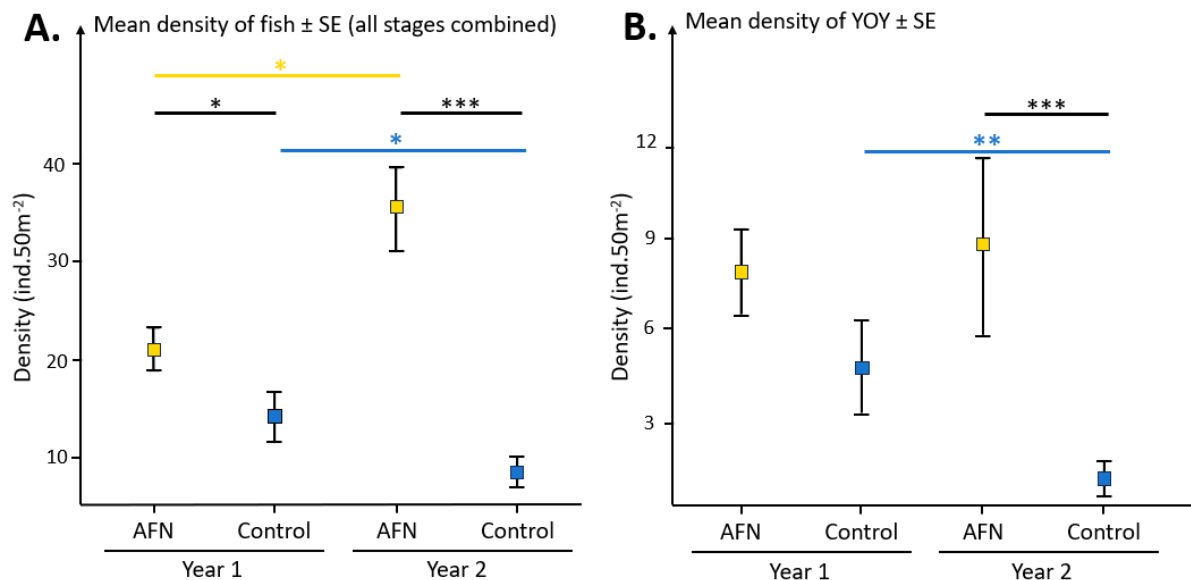
219 Table 1: Assessment of fish abundance for the two years of monitoring of the artificial fish
 220 nurseries (AFN) and the control docks. Numbers expressed in total abundance with YOY
 221 (Young of The Year) in parenthesis. Note that absolute values of Year 1 and Year 2 are not
 222 comparable due to unequal sample sizes (52 and 29 respectively).

223

Test: GLMer (Number ~ Year*Treatment)					
		Estimate	std.err	Z val	Pr(> z)
All stages	(Intercept)	3.043	0.116	26.13	< 0.001 ***

	Year	0.521	0.194	2.682	0.007	**
	Treatment	-0.397	0.169	-2.353	0.018	*
	Year:Treatment	-1.027	0.284	-3.615	< 0.001	***
Random effect		Variance	std.dev			
	Site	< 0.001	< 0.001			
YOYs						
	(Intercept)	2.079	0.205	10.17	< 0.001	***
	Year	0.077	0.347	0.222	0.824	
	Treatment	-0.54	0.299	-1.811	0.070	
	Year:Treatment	-1.454	0.534	-2.723	0.006	**
Random effect		Variance	std.dev			
	Site	< 0.001	< 0.001			
Test: GLHT (Number~Year_Treatment)						
		Estimate	std.err	Z val	Pr(> z)	
All stages						
	Year1_Control – Year1 AFN	-0.398	0.168	-2.365	0.018	*
	Year2_Control – Year2 AFN	-1.423	0.229	-6.227	< 0.001	***
	Year2_AFN – Year1 AFN	0.519	0.194	2.674	0.011	*
	Year2_Control – Year1 Control	-0.506	0.207	-2.442	0.018	*
	Year2_AFN – Year1 Control	0.917	0.197	4.649	< 0.001	***
	Year2_Control – Year1 AFN	-0.904	0.204	-4.430	< 0.001	***
YOYs						
	Year1_Control – Year1 AFN	-0.542	0.299	-1.811	0.098	
	Year2_Control – Year2 AFN	-1.996	0.442	-4.515	< 0.001	
	Year2_AFN – Year1 AFN	0.077	0.347	0.222	0.824	
	Year2_Control – Year1 Control	-1.377	0.406	-3.390	0.001	***
	Year2_AFN – Year1 Control	0.619	0.355	1.744	0.098	
	Year2_Control – Year1 AFN	-1.919	0.399	-4.813	< 0.001	***
Test: GLHT (Number~Year)						
		Estimate	std.err	Z val	Pr(> z)	
All stages						
	Year1 – Year2	0.510	0.194	2.674	0.008	**
YOYs						
	Year1 – Year2	0.077	0.347	0.222	0.824	

224 Table 2: Results of the GLMER model and GLHT post-hoc evaluating the effect of treatment
 225 and year of survey on All fish and Young Of the Year abundances.



226

227 Figure 4: Mean A.: fish densities and B.: Young Of the Year (YOY) densities (± standard error)
 228 on artificial fish nurseries (AFN) and the control docks (Control) during the two years of
 229 monitoring. (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

230

231 **3.2. Community analysis**

232 Treatment significantly influenced species richness with higher values on the AFN for all fish
 233 (13.6 ± 0.6 species.100 m⁻² on AFN vs 8.2 ± 0.6 species on control; GLMER.nb, z.value = -
 234 4.622, p < 0.001, Tab. 3) and YOYs (4.6 ± 0.4 species.100 m⁻² on AFN vs 2.0 ± 0.4 species
 235 on control; GLMER.nb, z.value = -4.159, p < 0.001, Tab. 3).

Test: GLMer (Species Richness ~ Year*Treatment)						
		Estimate	std.err	Z val	Pr(> z)	
All stages						
	(Intercept)	1.865	0.074	25.32	< 0.001	***
	Year	0.144	0.093	1.559	0.117	
	Treatment	-0.421	0.091	-4.622	< 0.001	***
	Year:Treatment	-0.265	0.154	-1.716	0.0861	
Random effect		Variance	std.dev			
	Site	0.006	0.081			
YOYs						
	(Intercept)	0.916	0.01	9.179	< 0.001	***
	Year	-0.243	0.183	-1.329	0.184	
	Treatment	-0.742	0.178	-4.159	< 0.001	***
	Year:Treatment	-0.582	0.377	-1.543	0.123	
Random effect		Variance	std.dev			
	Site	< 0.001	< 0.001			

236 *Table 3: Results of the GLMer model testing for the effect of Year and treatment on species*
 237 *richness for all fish and Young Of the Year (YOY).*

238 Treatment (AFN, Control) and year of monitoring (Year 1, Year 2) significantly influenced fish
 239 community structure for all stages (PERMANOVA, R² = 0.104, p < 0.001 and R² = 0.026, p =
 240 0.002) and for YOYs (PERMANOVA, R² = 0.028, p = 0.004 and R² = 0.038, p < 0.001) (Fig. 5
 241 and Tab. 4). The interaction between these two factors had a significant influence on
 242 community structure for all stages (PERMANOVA, R² = 0.023, p < 0.001, Tab. 4) but not for
 243 YOYs (PERMANOVA, R² = 0.013, p = 0.22). The pairwise PERMANOVA revealed that all
 244 possible interactions of treatment and year of monitoring were significantly different from each
 245 other (pairwise PERMANOVA; R² > 0.03, p < 0.01, Tab. 4) for all life stages.

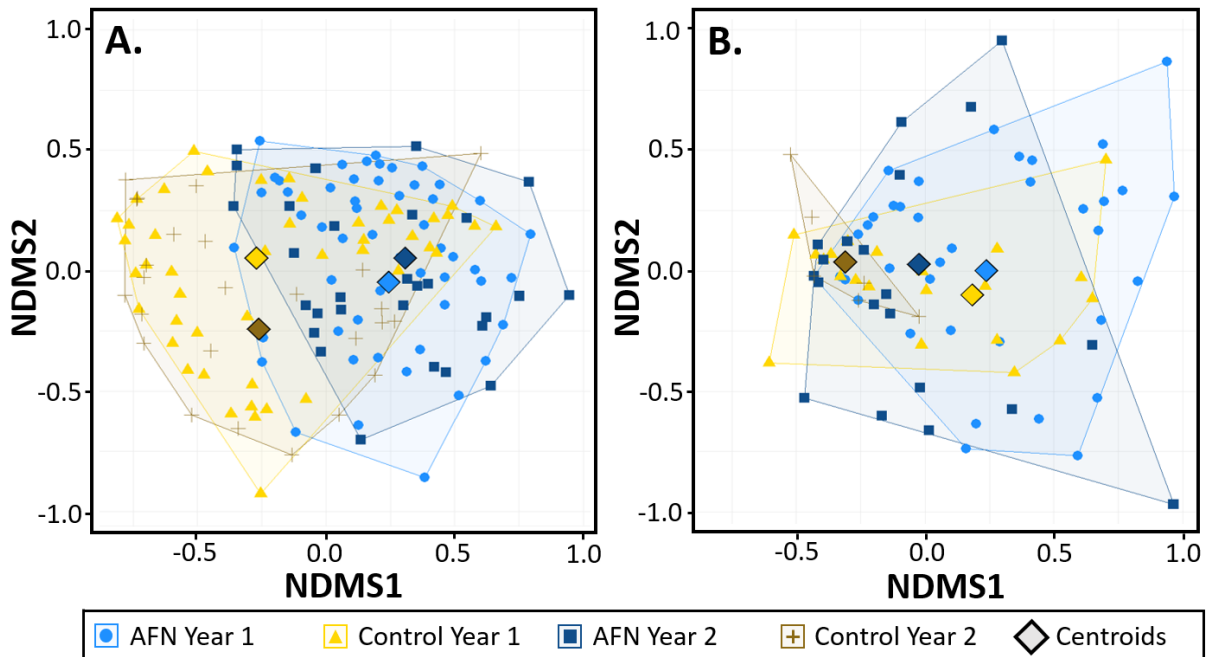
246

Test: PERMANOVA (Dist.matrix ~ Treatment * Year)							
		Df	Sum of Sqs	R2	F	Pr(>F)	
All stages							
	Treatment	1	4.747	0.105	18.75	0.001	***
	Year	1	1.196	0.027	4.723	0.001	***
	Treatment:Year	1	1.026	0.023	4.051	0.001	***
	Residual	152	38.48	0.847			
	Total	155	45.45	1.000			
YOYs							
	Treatment	1	0.711	0.028	2.924	0.004	**
	Year	1	0.954	0.038	3.923	0.002	**
	Treatment:Year	1	0.319	0.013	1.311	0.219	
	Residual	96	23.35	0.922			
	Total	99	25.34	1.000			
Post-Hoc test: Pairwise-PERMANOVA							
		Df	Sum of Sqs	R²	F-Model	Pr(>F)	p.adjust
All stages							
	Year1_Control – Year1 AFN	1	2.015	0.071	7.528	< 0.001	< 0.001 ***

Year2_Control – Year2 AFN	1	3.758	0.239	16.62	< 0.001	< 0.001	***
Year2_AFN – Year1 AFN	1	1.382	0.072	6.239	< 0.001	< 0.001	***
Year2_Control – Year1 Control	1	0.839	0.039	2.910	0.007	0.007	**
Year2_AFN – Year1 Control	1	3.265	0.144	12.57	< 0.001	< 0.001	***
Year2_Control – Year1 AFN	1	3.166	0.143	12.83	< 0.001	< 0.001	***

247 Table 4: PERMANOVA and associated post-hoc Pairwise PERMANOVA outputs testing the
 248 fish community across each treatment and year

249

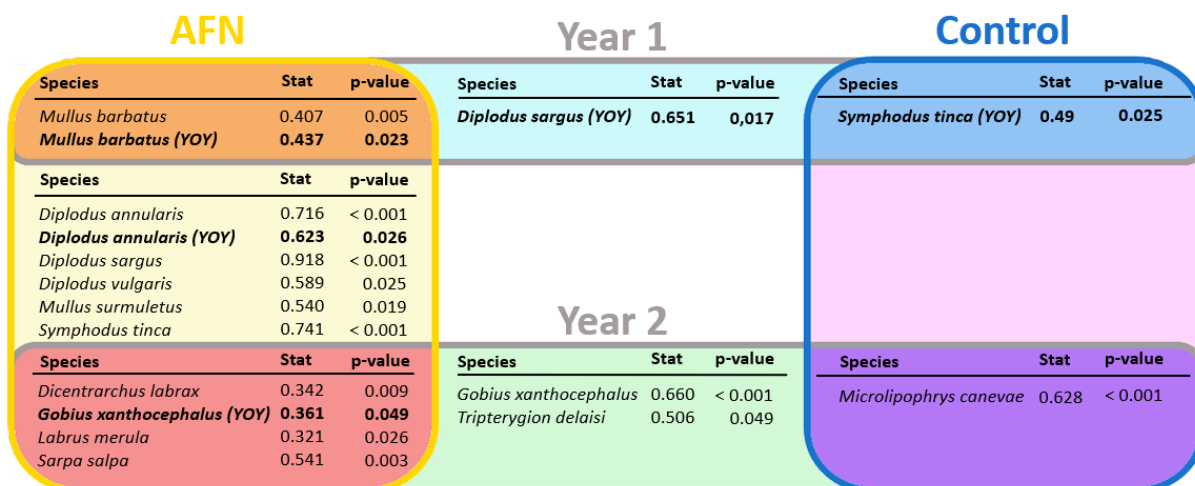


250

Figure 5: Non-metric Multidimensional Scaling (NMDS) of the fish community structure for each treatment and year for A) All stages and B) Young of the Year (YOY).

251

252 Indicator species analysis revealed 5 species to be associated with the AFN as well as YOYs
 253 of the species *Diplodus annularis* (Multipattern analysis, stat > 0.54, $p < 0.026$; Fig. 6). No
 254 species was identified as being associated with the control. YOYs of the species *Diplodus*
 255 *sargus* were associated with the first year of monitoring, and two species were associated with
 256 the second year of monitoring (Multipattern analysis, stat > 0.51, $p < 0.049$; Fig. 6). At least
 257 one species or YOY species was associated with each interaction term (Fig. 6).



259 Figure 6: Venn diagram of the indicator species (multipattern analysis) for each year and
 260 treatment. The association statistic (Stat) and p-value are given for each indicator species.
 261 YOYs are in brackets and in bold.

262 **3.3. Estimation of the predation rate**

263 Loss of squid baits to predators varied among treatments and predation intensity was
 264 significantly higher on controls compared to AFNs (Nested Cox, Hazard-ratio = 64.7%; Z = 4.1,
 265 p < 0.001; Figure 7). Nearly all the squidpops deployed on controls were consumed within 3 h,
 266 whereas almost 40% of them remained on the AFNs. By 6 h, however, most baits had been
 267 consumed in both treatments.

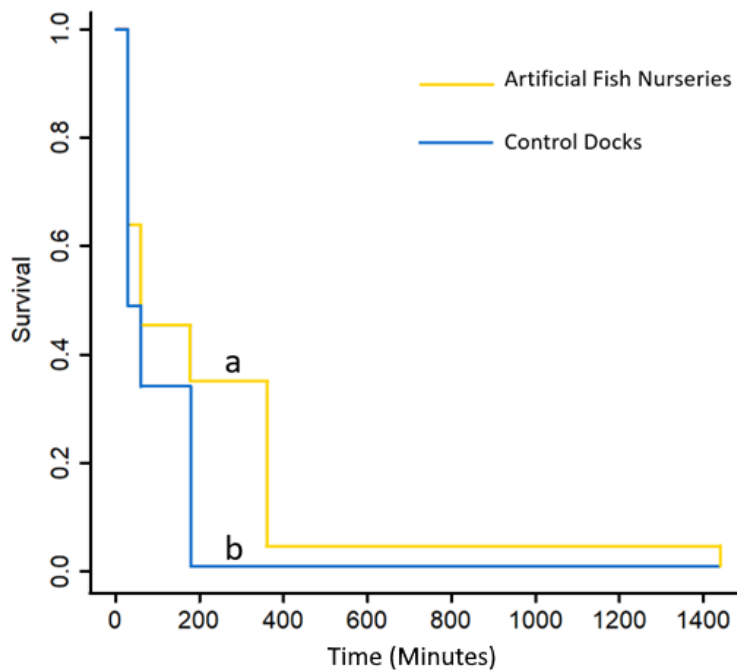


Figure 7: Kaplan-Meier survival curves of bait as proxy of predator activity. Lower-case letters indicate significant differences between sites (Nested Cox; Hazard-ratio = 64.7%, $Z = 4.1$, $p < 0.001$).

270 4. Discussion

271 Ecological restoration is aimed at assisting the recovery of a degraded or damaged ecosystem
 272 (Clewell and Aronson, 2013). Where degradation cannot be reversed, rehabilitation to the
 273 highest practicable ecological functionality and increasing similarity to the reference ecosystem
 274 are often favored (McDonald et al., 2016). Considering ports are irreversibly degraded coastal
 275 ecosystems, eco-engineering approaches like artificial habitat units may help to improve the
 276 ecological performance and can be part of ecological rehabilitation projects (Komyakova et al.,
 277 2019). Various solutions have been proposed all around the world to improve their ecological
 278 status by attempting to increase benthic biodiversity (Bishop et al., 2022; Firth et al., 2014;
 279 Strain et al., 2020; Vozzo et al., 2021) and rehabilitate their fish nursery function (Astruch et
 280 al., 2017; Bouchoucha et al., 2016; Mercader et al., 2017; Patranella et al., 2017; Strain et al.,
 281 2018). However, up to now these potential solutions have remained at a very experimental
 282 scale and research on their success remains scarce or is often driven by economic and/or
 283 regulatory factors (Firth et al., 2020). Here, we aimed to improve knowledge of the potential
 284 benefits of Artificial Fish Nurseries (AFN) on fish abundance in marine urban habitats, by
 285 monitoring AFNs installed in a large port in the northwestern Mediterranean Sea for two years.
 286 While our study still lacks in terms of optimal experimental design, duration or scale it may still
 287 contribute to better understand the function such AFNs may provide. In accordance with our
 288 initial hypotheses, AFNs had higher densities of fish over the whole study duration. However,

289 densities of Young of the Year (YOYs) were higher on the AFN only during the second study
290 year compared to bare docks. AFN hosted a greater diversity of fish overall. Community
291 structure varied over treatments and years. Predation intensity was lower on AFNs.

292 The carried-out monitoring showed that fish densities were more than two times higher on
293 AFNs than on bare docks for all life stages combined as well as for YOYs. This higher density
294 was significant for both study years for all life stages and for YOYs in the second year of the
295 study. It should be noted that this difference between the two treatments is significant whereas
296 fish abundance and biodiversity may be underestimated on AFNs. The AFNs were colonized
297 by benthic fouling communities, which may increasingly hinder a reliable count of local fish
298 populations, which was not the case on control. However, great care was taken to avoid this
299 bias and other ecological processes may also explain these observations. Therefore, it seems
300 that the addition of structural complexity by the AFNs led to an increase in fish density. This is
301 consistent with previous results obtained with other types of AFNs, which have already
302 demonstrated their ability to increase fish abundance and to partly participate in the
303 rehabilitation of the nursery function in ports (Bouchoucha et al., 2016; Mercader et al., 2017;
304 Patranella et al., 2017). A study carried out in the same region showed a two-fold increase of
305 YOYs on AFNs compared to areas without AFNs (Bouchoucha et al., 2016). This order of
306 magnitude is strikingly similar to those observed in our study. This may indicate that AFNs
307 might be an effective tool for increasing fish and YOY abundances in marine urban habitats,
308 potentially by rehabilitating part of the nursery function lost during urbanization.

309 Here, the overall densities of YOY abundances slightly decreased between Year 1 and Year 2
310 due to a significant decrease in YOY abundance on control. Inter-annual variability in fish
311 settlement and juvenile assemblages has already been shown in natural areas (Anderson,
312 1988; Beraud et al., 2018; Félix-Hackradt et al., 2013; Hogan et al., 2012) as well as in port
313 areas (Bouchoucha et al., 2016). The variation of propagule production is generally the
314 determining process for these differences (Di Franco et al., 2012; Faillettaz et al., 2020; Planes
315 et al., 1998) and is highly dependent on the physico-chemical characteristics of the local water
316 column (O'Connor et al., 2007; Ottmann et al., 2018; Tanner et al., 2017). They can also be
317 explained by the match/mismatch hypothesis (Cushing, 1990), where a time lag between the
318 larval phase of the fish and the presence of their planktonic food may be a cause of increased
319 mortality (Di Franco et al., 2015; Hidalgo et al., 2009). This discrepancy between the control
320 group, which experienced a significant decrease in YOY abundance between both years, and
321 the AFN treatment, where YOY abundance remained constant, cannot be fully explained by
322 interannual variation alone. The observation might be attributed to stochasticity, as even in
323 natural habitats, the abundance of juveniles within nurseries does not consistently remain
324 constant. In fact, previous studies have documented interannual variability in the distribution

325 of post-larvae within nursery sites, both on a large and small scale (Victor, 1986). More
326 troubling, however is the possibility that AFNs could act as concentrators for YOYs and do not
327 effectively increase the population (Bohnsack and Sutherland, 1985; Grossman et al., 1997).
328 While our experimental design does not allow to precisely show it, a concentrator effect for
329 YOY would imply that those that would have been present on the control docks have settled
330 preferentially on the AFNs, gradually increasing in these areas while decreasing in others, with
331 potentially no net benefit in terms of population size. This could potentially be what can be
332 observed when considering all fish sizes, as their abundance significantly increased on the
333 AFNs, while it decreased on controls between the two years of monitoring. This reflection on
334 fish attraction versus fish production of AFNs is a recurrent question when trying to assess the
335 efficiency of AFNs (Bouchoucha et al., 2016; Mercader et al., 2017) and more generally that
336 of artificial reefs (Cresson et al., 2019; Grossman et al., 1997; Pickering and Whitmarsh, 1997).
337 It is obviously impossible to draw definitive conclusions from these observations alone and it
338 is important to note that attraction versus fish production characteristics of artificial fish habitats
339 are not mutually exclusive (Pickering and Whitmarsh, 1997; Roa-Ureta et al., 2019; Smith et
340 al., 2015). Future studies should focus their designs on this question as it seems crucial for the
341 overall fish population benefits of these eco-engineering strategies.

342 The structure of the communities and the species observed on the AFN were similar to the
343 observations made in other port areas (Clynick, 2006; Mercader et al., 2017). However,
344 surveys carried out in natural areas close to Toulon Bay, such as the Iles des Embiez and Cap
345 Sicié (Couvray, 2020) and in the Port Cros National Park (Astruch et al., 2018; Francour, 1997)
346 show greater taxonomic diversity and pelagic fish (excluding *Blenniidae*, *Gobiidae* and
347 *Tripterygiidae*) compared to our study (> 47 species as opposed to 28). The addition of AFNs
348 on port structures seems to increase species richness by adding complexity to the environment
349 (Santos and Monteiro, 1997) and seems to have a fish community more similar to those
350 observed in natural environments (Paxton et al., 2020). We indeed noted a higher fish diversity
351 on AFNs than on control docks, however we did not monitor natural environments, which does
352 not allow making a direct comparison in terms of community structure. Nonetheless,
353 community structure was significantly different between AFNs and control docks and between
354 the two years of monitoring for all fish and for YOYs. This result is also expressed in the
355 changes observed in indicator species associated with the two main effects (Treatment, Year).
356 This observation may be the result of the substrate differences between the two treatments.
357 The substrate is an element likely to influence the structure of the communities at a site. In the
358 natural environment, different fish and YOY communities can be observed depending on the
359 nature of the bottom (Cheminée et al., 2021; Di Lorenzo et al., 2016; Luckhurst and Luckhurst,
360 1978). This observation has also been made for different artificial substrates (Cheminée et al.,

361 2021; Mercader et al., 2017). Particularly noteworthy here: juveniles of the species *Diplodus*
362 *annularis* were found as an indicator species for the AFN substrate compared to the control
363 substrate. The greater presence of this species on AFNs than on docks in port areas has
364 already been noted in previous studies (Bouchoucha et al., 2016; Mercader et al., 2017), which
365 implies that for this species in particular the AFN seem to be a suitable habitat. We also
366 observed significant changes in community structure between Year 1 and 2 for all stages and
367 YOYs. The interannual difference between communities can be explained by the variability of
368 abiotic factors, which are known to strongly influence the establishment of fish communities
369 (Ajemian et al., 2015). The fact that the densities of YOYs did not differ between the two
370 treatments during Year 1 and became significantly different during Year 2 may be indicative of
371 a maturation of the AFNs in their function as fish nurseries (Becker et al., 2018; Charbonnel et
372 al., 2002; Cresson et al., 2019). The residence time of AFNs in the environment allows fish
373 communities to develop, leading to a temporal increase in the specific diversity of such
374 structures (Cresson et al., 2019). It is still too early to conclude on this observation, but further
375 monitoring would allow verifying this result.

376 The Squidpop assay showed less predation on the AFNs than on bare docks with a 64.7% risk
377 decrease on AFNs, and this despite higher abundance and diversity of potential prey items
378 (juveniles). The imitation of seagrass beds by the AFNs provides hiding places used by fleeing
379 prey (Thiriet et al., 2022), allowing for greater survival success. Habitat complexity has been
380 demonstrated to diminish the impact of predation on prey fish on numerous occasions (Almany,
381 2004; Heck Jr. and Orth, 2006; Jones et al., 2021). However, as our squid baits were unable
382 to actively flee, the higher survival observed here may indicate that predators might avoid AFNs
383 due to lower predation success. Predators that have lower foraging success in complex
384 habitats (Gotceitas and Colgan, 1989; Warfe and Barmuta, 2004) might avoid such areas in
385 order to optimise foraging (Eklöv and Diehl, 1994; Sims et al., 2008). This might indicate that
386 the increase of 3D complexity through AFNs reduces predation intensity and might thus
387 increase juvenile fish survival. Unfortunately, here the predators causing the attacks on squid
388 baits could not be precisely identified. However, past studies indicate that *Sparidae* might be
389 the most prolific predators in marine urban habitats (Gauff et al., 2022; Oricchio et al., 2016;
390 Rodemann and Brandl, 2017). This may mean that one of the essential functions of a nursery
391 (Beck et al., 2001) was potentially partially rehabilitated in our study. However, one should
392 note that the habitat features that optimize the probability of survival of fish juveniles depend
393 on the species considered (Mercader et al., 2019). Moreover, over time AFNs are colonized
394 by different benthic species (Gauff et al., 2023). It is possible that the presence of these
395 organisms provides an abundant food source for generalist predatory fish, which could result
396 in a decrease in the predation rate on AFNs. The presence of this fauna on the AFNs can be

397 beneficial as it is a source of food for potential predators as well as juvenile fish (Saulnier et
398 al., 2020; Tableau et al., 2019). However, this colonization can also be associated with
399 negative side effects like providing refuges for introduced species (Gauff et al., 2023).

400 Our study demonstrated the potential benefits of installing AFNs in view to rehabilitating the
401 fish nursery function in port areas. We have shown that AFN structures host a higher
402 abundance of fish, including YOYs, than bare docks, with increased fish biodiversity and lower
403 predation intensity. Although we are unable here to precisely identify the processes
404 responsible for these observations, AFNs seem to partly fulfil the definition of a nursery by
405 sheltering a greater abundance of juvenile fish and protecting them against predation (Beck et
406 al., 2001; Dahlgren et al., 2006). Although our results concern only a specific port area and
407 one type of AFNs and, unfortunately, lack the initial state before the rehabilitation action, they
408 agree with an increasing number of studies showing similar results (Astruch et al., 2017;
409 Bouchoucha et al., 2016; Lapinski et al., 2017; Mercader et al., 2017; Patranella et al., 2017).
410 However, although this approach appears promising, there are still many uncertainties
411 regarding the functionality and efficiency of such structures and further studies should be
412 carried out. The hypothesis of the complete rehabilitation of the nursery function in port areas
413 by AFNs can only be confirmed once the effective connectivity between juvenile fish present
414 on AFNs and adult populations has been demonstrated and quantified. Furthermore, it remains
415 essential that the potential benefits of ecological rehabilitation methods are weighed against
416 the potential problems they might cause (Firth et al., 2020; Gauff et al., 2023; Schaefer et al.,
417 2023), as they may also provide ecological disservices such as being a refuge for non-
418 indigenous species (Gauff et al., 2023). In addition, the ropes making up the AFNs in this study
419 are composed of polypropylene. Plastic pollution presents a global environmental challenge
420 (Li et al., 2021; Moore, 2008; Welden, 2020). As nations worldwide strive to minimize plastic
421 waste in marine environment (Horejs, 2020; Jia et al., 2019), it can be contradictory to advocate
422 for the use of plastic structures in habitat restoration initiatives. These materials are generally
423 used for their very high mechanical resistance but in the marine systems, they have the
424 potential to fragment into smaller plastic particles known as microplastics and nanoplastics
425 (Andrady and Zhu, 2021; Sipe et al., 2022) causing both impacts on marine organisms and
426 human health issues (Cho et al., 2019; Rezanian et al., 2018). Additionally, they can release
427 plasticizers (such as di-(2-ethyl hexyl) phthalate) into the surrounding environment (Gunaalan
428 et al., 2020). These impacts alone should be sufficient evidence to abandon their use in
429 restoration programs. Moreover, plastic structures are also typically at risk of invasion by non-
430 native species for several reasons, including open niche opportunities. Rather than enhancing
431 habitat quality for native species, plastic habitat structures can favor colonization and
432 establishment of non-native species (Glasby et al., 2007; Pinochet et al., 2020). It is therefore

433 important to ensure that the benefits of AFN are not outweighed by greater negative effects.
434 Whatever the case, public policies should include the management and protection of natural
435 fish nurseries before considering ecological engineering as a solution.

436 **Acknowledgements**

437 We wish to thank the port authorities for authorizing access for monitoring. We also wish to
438 thank the company Seaboost for providing the AFNs for this study. We are grateful to Olivier
439 Dugornay for his photography. In addition, we wish to acknowledge the anonymous reviewers
440 for their valuable comments and suggestions that improved our manuscript.

441 **Author contributions**

442 **Etienne Joubert:** Methodology, Formal analysis, Investigation, Writing – Original Draft,
443 Visualization; **Robin P.M. Gauff:** Conceptualization, Methodology, Investigation, Formal
444 analysis, Resources, Writing – Review & Editing; **Benoist de Vogüé, Christophe Ravel, and**
445 **Fabienne Chavanon:** Investigation; **Marc Bouchoucha:** Conceptualization, Methodology,
446 Investigation, Writing – Review & Editing, Project administration, Funding acquisition;

447 **Financial support**

448 This research was funded by the IFREMER institute.

449 **Conflict of interest**

450 The authors declare that they have no known competing financial interests or personal
451 relationships that could have appeared to influence the work reported in this paper.

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