

The effect of predation on artificial reef juvenile demersal fish species

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Abstract There is a concern that artificial reefs (AR) may act purely as fishing aggregation devices. Predators attracted to ARs can influence the distribution and abundance of prey fish species. Determining the role of predators in AR is important in advancing the understanding of community interactions. This paper documents the effects of predation on fish assemblages of AR located near a coastal lagoon fish nursery. The *Dicentrarchus labrax* is a very opportunistic species preying on juveniles (0⁺ and 1⁺ age classes) of several demersal fish species on the ARs. Reef prey and sea bass abundance were negatively correlated. The mean numbers of prey per sea bass stomach increased with the increase of reef fish prey abundance, suggesting that predation has a significant influence, resulting in a decrease in prey abundance. Prey mortality (4–48%) of demersal reef fish associated species depends on bass density. Prey selection was related both with prey abundance and vulnerability. Results showed that *D. labrax* predation on AR-fish associated species can increase prey natural mortality. However, the role of bass predation on the ecological functioning of exploited ARs is not clear. There may be increases in local fishing yields due either to an increase in predator biomass through aggregation of sea bass attracted to ARs or to greater production. In contrast, predation on juveniles of economically

important reef fish preys, especially the most frequent and abundant (*Boops boops*), can contribute to a decrease in recruitment to the fishery. Our results indicate that inter-specific interactions (predator–prey) are important in terms of conservation and management, as well as for the evaluation of the long-term effects of reef deployment. Thus, it is necessary to consider ecological interactions, such as predation, prior to the development and deployment of artificial habitats as a tool for rehabilitation.

Introduction

Populations of marine fishes are often characterized by dramatic fluctuations in abundance. However, the causes of such variations are difficult to measure and quantify due to the different scale effects that natural and anthropogenic factors may have on the ecosystem. Most of the studies at the ecological level to date have directly or indirectly concerned the question of whether reef fish assemblages are structured by competition or recruitment limitations (Hixon 1991). The debate concerning the dynamics of reef fish populations has centred on the relative contributions of density-independent factors acting during larval dispersal and density-dependent processes following the larval stage (Hixon et al. 2002; Hixon and Webster 2002). Although a growing number of field studies have documented density-dependent mortality in reef fish populations (Hixon and Webster 2002; Hixon and Jones 2005), very few studies have identified the actual mechanisms and conditions responsible for these patterns (Hixon and Carr 1997; Forrester and Steele 2000; Anderson 2001).

Abrams (1987) demonstrated that the interaction between prey and predator species could be positive,

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negative or neutral, depending on the population dynamics of the predator and prey species involved. The idea that fish predation can strongly affect the distribution and the abundance of prey species within a community, is a central tenet of modern ecology (Hixon and Beets 1993). It is often hypothesised that predation can significantly reduce the abundance of juvenile fish attracted to reefs for refuge or feeding, and this may lead to a reduction of total biomass (Hixon 1991; Stewart and Jones 2001; Stewart and Connell 2002). However, evidence of predation and its direct effects is difficult to obtain in most systems.

Artificial reefs (AR) are deployed worldwide with a number of goals, including the mitigation of habitat (coral reefs) loss, enhancement of fish and bivalve catches (Bohnsack and Sutherland 1985; Monteiro and Santos 2000), and habitat protection (Bayle-Sempere et al. 1994). Since ARs are very efficient aggregation tools (Bohnsack and Sutherland 1985; Polovina 1991), there is a concern that greater natural mortality of prey may result from high concentration of predators. Predation may play an important role in artificial habitats, with the structure of the food web controlled by the biodiversity within the system and/or by top predators (top-down control). Although predation was proposed as an important structuring factor in the 1970s (Hixon 1991), it has received little attention as far as AR studies are concerned. From both management and biological perspectives it is necessary to consider the secondary/indirect effects of predation on the environment, prior to the development of artificial habitats as a tool for rehabilitation.

Most fish predation studies in reefs have focused on predator–prey relationships between resident predator and prey species and the role of reefs in providing shelter from predation (Shulman 1985a, b; Hixon and Beets 1993; Hixon and Jones 2005). However, few studies have examined the influence of transient predators on reef fish assemblages, mainly because of the difficulty in assessing predator pressure of this nature (Carr and Hixon 1995).

Dicentrarchus labrax Linnaeus (common sea bass), an important transient predator that had rarely been observed on the Faro AR (deployed in 1990) in the 15 years following deployment (Santos et al. 1995a, 2005) has been recorded frequently and abundantly since the enlargement of the artificial reef system in 2003 (Francisco Leitão unpublished data).

Given the lack of resident piscivores and the dominance of the sea bass in terms of biomass on the reefs (Francisco Leitão unpublished data), it was hypothesized that this transient predator could have a significant impact on AR prey species. Predator density may lead to increased consumption of prey as a result of more predators consuming more prey in total. It has been recognized that piscivorous predatory fish species are more likely to respond to larger aggregations of prey (Stewart and Jones 2001; Connell

2002). This may cause an increase in the proportional mortality of aggregated prey, since the predators may feed at a greater rate (Connell 2000, 2002). Such feeding behaviour may not only destroy the protection afforded to fish in larger schools, but it may also cause greater per capita mortality in larger schools (density-dependent mortality), consequently resulting in the reduction of prey abundance (Connell 2000; Stewart and Jones 2001). More directly, inverse relationships have been noted between the local abundances of prey fish and resident piscivores in natural rocky and coral reef areas (Shulman et al. 1983; Shulman 1985a, b; Hixon and Beets 1989; Hixon and Beets 1993; Overholtzer-McLeod 2006; Johnson 2006).

This paper documents the effects of predation in structuring AR reef fish assemblages. We tested whether *D. labrax* (top predator) affects the structure of demersal artificial reef fish assemblages. First, we evaluated the relationship between predator and prey abundances. Second, we quantified the number of prey consumed by the predator when prey numbers varied. Third, the influence of predator abundance on prey mortality was studied. Finally, the question of predator preferences was examined.

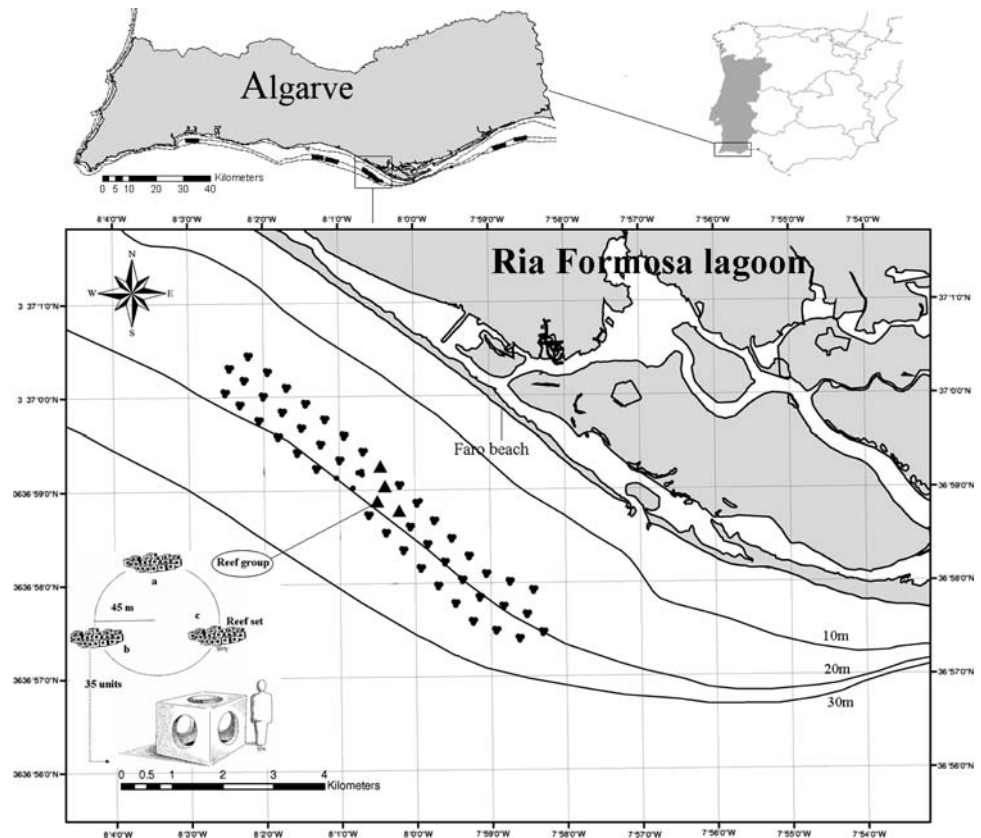
Materials and methods

Study area

In the south coast of Portugal (Algarve) multi-purpose ARs have been constructed and deployed since 1990. Their deployment aimed to increase the amount of hard bottom habitat, which is scarce on the southern grounds, to provide suitable habitat and protection for juvenile fish that annually migrate from the lagoon systems located along the southern coast, to promote biodiversity and to increase fishing yields (Monteiro and Santos 2000).

The sampling site chosen for this study was the Faro/Ancão artificial reef system (Lat 36°59.25'; Long 8°00.43') 4 km off the Ria Formosa lagoon, an important nursery area (160 km²) that supplies juvenile fishes to nearby coastal waters (Fig. 1). Four AR groups were surveyed, specifically FP1_{a,b,c}, FP3_{a,b,c}, FP5_{a,b,c} and FP7_{a,b,c}, deployed in 1990 off Faro beach (Algarve, Southern Portugal) on clean sandy grounds (few natural rocky areas nearby) at depths of approximately 21–23 m. These ARs were selected since we assume that they have been fully colonized by reef fish assemblages (Santos et al. 2005). Given the distance between reef groups (~300 m), these were considered to be independent sampling locations. Each artificial reef group comprises three reefs sets, with 35 concrete cubic units each, organized in a two-layer pyramid (Fig. 1). Each reef set occupies an area of approximately 132 m² corresponding to 529 m³ in water volume (Santos 1997).

Fig. 1 Algarve artificial reef complex, study site, i.e. Faro/Ancão AR system (large triangles are AR groups where data were collected), the reef modules and their spatial and structural organization



Methodology

The understanding of the trophic relationship between the *D. labrax* and the AR fishes necessarily requires knowledge of changes in predator and prey abundance within the AR and the diet of the predator.

To characterise predator–prey assemblage abundance changes, a long-term study (from August 2003 to September 2004) using visual censuses was carried out on a monthly basis. Data were recorded by scuba divers who documented size, density and behaviour (feeding and site fidelity of the species). The stationary point count technique as described by Santos et al. (2005) was used. The same diver recorded the data with an underwater writing pad, always. During each trial the diver sampled all three-reef sets of each reef group. In each reef set, three independent random counts were carried out. As daily variation of reef fish fauna is found in these ARs (Santos et al. 2002), the visual censuses were always carried out between 9:00 and 12:00 a.m. and under similar tide conditions.

Sea bass specimens were collected by spear fishing every month from October 2003 to September 2004, except for February due to rough sea conditions. This method increases the probability of prey identification and guarantees that fish were collected in the AR. In order to

associate predators with prey (diet), sea bass were caught immediately after the census by a second diver and once onboard placed in ice in order to stop digestion. At the laboratory, the total length (cm) of each specimen was recorded. After removal, the stomachs were fixed in a 4% formaldehyde solution during 48 hours. After washing with running water, the stomach contents were sorted under a stereoscopic lens. All prey items were separated by *taxon*, counted and weighed to the nearest 0.01 g. Depending on the state of digestion, prey items were identified to the lowest possible taxonomic level.

Statistical analysis

Species with high site fidelity, such as cryptic and sedentary species, which generally take a stationary position in the AR or on the bottom around it, were defined as residents (e.g. Blennidae) and species that do not shelter in AR units and that show a swarming response to the reef, (e.g. *Boops boops*) upon the approach of piscivores or divers were designated as reef-associated species. Reef-associated species are those that occurred within a distance of approximately 1.5 m to the reef as recorded during the visual censuses.

Stomach content analysis

The frequency of occurrence (FO), calculated as a percentage of the number of stomachs with prey divided by the number of stomachs with items, and the percentage in number (%N) and weight (%W) (Hyslop 1980) were used to assess diet composition of the sea bass. The most important food items were determined using the feeding coefficient ($Q = \%N \times \%W$), which characterizes the relative importance of the different preys in a diet (Hureau 1970). Using Q , the prey was separated into three categories (principal prey, $Q > 200$; secondary prey, $20 < Q < 200$; occasional prey, $Q < 20$). The index of relative importance (IRI) (Pinkas et al. 1971) was also estimated, $IRI = (\%N + \%W) \times FO$. The measurement of the stomach fullness (Full stomach $\geq 75\%$; quite full 50–74.9%; half-full 25–49.9%; almost empty 5–24.9%; empty 0–4.9%) and prey digestion state was carried out according to Sigurdsson and Astthorsson (1991). Predation (%) was calculated based on the monthly data as the number of times sea bass fed on AR fish prey species, when both sea bass and prey species were simultaneously observed in the AR group reef set. Predation validation was made in the laboratory after checking if predators had the prey species observed in the AR in their stomachs.

Predator–prey relationships

Several hypotheses concerning prey–predator relationships were tested based on the visual census and stomach-content data, and the assumption that there are no resident AR piscivores:

1. The first approach examined the relationships between prey and predator abundances (Hypothesis I):

Ho: there is no relationship between sea bass and prey abundances.

H_A : there is a relationship between sea bass and prey abundances.

The relationships between predator and prey abundances were analysed through Spearman correlations (Zar 1996). If predation is the predominant process regulating the number of reef-associated prey, then there should be a negative correlation between the mean number of predators and the mean number of prey per reef averaged over all censuses. Mean density of both *D. labrax* and the reef prey species found in the stomach contents of the sea bass were calculated by averaging monthly reef set data counts. Given that the data were based on visual census methods, a probability level $\alpha = 0.1$ was used in all analyses in order not to reject the null hypothesis when this is true (Type II error).

2. The second approach was to quantify the number of prey consumed (diet) by the predator when AR prey numbers varied (Hypothesis II):

Ho: There is no relationship between the numbers consumed and the number of prey available.

H_A : There is a relationship between the numbers consumed and the number of prey available.

Visual census data and stomach data were used in order to evaluate if predation is influenced by the abundance of the AR available reef fish prey. Regression analysis was carried out between mean reef set prey abundance per month (independent variable) and the mean number of preys per stomach.

3. If bass predation influences the number of reef-associated prey–fish, then there should be a positive relationship between the mean number of predators and the mortality of prey (Hypothesis III):

Ho: There is no relationship between prey mortality and the number of predators.

H_A : There is a relationship between prey mortality and the number of predators.

Prey mortality, $M(\%)$, was estimated as follows:

$$M(\%) = (CN_i/TN_i) \times 100 \quad (1)$$

where CN_i is the number of prey i consumed, calculated as the product of the mean number of prey i per bass stomach (a_i) and the total number of bass (b) observed on the reef ($CN_i = a_i \times b$), and TN_i is the estimated total number of prey species i on the reef, that is calculated as the sum of the estimated total number of prey i consumed on the reef and the number of species i on the reef estimated by visual census. Given the condition of the prey species in the bass stomachs, it is assumed that predation is recent and took place at the reef where the prey and predator species were quantified. Regressions were carried out between the monthly prey mortality (%) and predator mean monthly abundance per reef set.

4. Finally, the question of predator preferences was examined (Hypothesis IV):

Ho: The bass has no preference.

H_A : The bass is a selective feeder.

Ivlev's index (Ivlev 1961) was used as a measure of electivity (E) for the reef fish species in the fish diet: $E = (d_i - p_i)/(d_i + p_i)$ where d_i is the % of food item in the diet, and p_i is the % of food item in the environment. The mean Ivlev's electivity index, and standard deviation, were calculated using the monthly data. Values of Ivlev's electivity index range from -1.00 (complete avoidance) to $+1.00$ (exclusive selection). The p_i contribution of the

different fish prey items in the AR was estimated. This was possible because visual census observations were carried out monthly for the whole reef fish assemblage. Nevertheless, considering the aim of the study, only information regarding fish species was used in electivity index estimation.

Results

Predator diet

A total of 74 sea bass specimens were caught, comprising 46 males, 26 females and two of undetermined sex. Their total lengths ranged from 33 to 74.2 cm, with a mean value of 47.1 ± 10 cm.

A total of 17 stomachs (23%) were empty. A total of 142 prey items were found and identified in the remaining stomachs (57). The mean number of items found per stomach was 2.5. Full stomachs and quite full stomachs represented 5 and 36%, respectively. The remaining stomachs sampled were half full and almost empty, representing 33 and 26%, respectively. The majority of preys found in the stomach contents were very easy to identify (69%), having been recently ingested or showing an early phase of digestion. In fact, of the above proportion 31% of the items were assigned as non-digested (partially intact items) and 38% as slightly digested.

Sea bass diet was composed of a low variety of food items, including crustaceans, gastropods and finfish (Table 1). Crustaceans and fishes were the items

contributing most to the sea bass diet, as far as the number (*N%*) and weight (*W%*) of prey is concerned (Table 1). The most important taxonomic groups (*Q* and *IRI*) contributing to the sea bass diet were the crab *Polybius henslowi* Leach (principal prey) and several reef-associated demersal fish species. The latter include *Boops boops* Linnaeus (principal prey), *Pagellus acarne* Risso and *Scomber japonicus* Houthuym (secondary preys), and *Trachurus trachurus* Linnaeus (occasional preys). The bass diet also includes resident species belonging to the Blenniidae family (occasional preys). Moreover, the stomach content of sea bass also revealed hard reef-associated species such as *Necora puber* Linnaeus (Table 1). However, the most frequently observed items were *B. boops*, *S. japonicus* and *P. acarne*. The most important prey in numbers (*N%*) were *B. boops* and *S. japonicus* (Table 1), with the latter having a greater mean length (Table 2) and thus contributing more in weight (*W%*) to predator diet than the other fish species (Table 1).

Prey–predator behaviour

In situ observations found that sea bass swims both around and in the inner part of the AR (top, middle and bottom layers of the AR). In relation to reef fidelity the sea bass was categorized as a transient species. Although the sea bass was observed entering the ARs to avoid divers, they usually leave after 5–10 min, probably due to the stress induced by the presence of the divers.

All the associated reef fish species found in the sea bass stomachs, except the blennies (resident species) were demersal (mid-water) species. These prey species showed a relatively wide home range, moving throughout the external reef area, in the middle and top layers. When disturbed by divers or by the presence of the sea bass, these species never take refuge within the ARs.

Predator–prey assemblage structure and variations in abundance

The frequency of occurrence of sea bass was high (86%) with a mean number of 55 individuals per reef set and a mean total length class of 40 cm that was slightly below the size at first maturity (Table 2). The most frequently occurring prey species found in the ARs were *B. boops* and blennies, with both *taxa* being observed in all counts (Table 2). The frequency of occurrence of *P. acarne* was also high, 54% (Table 2), while *T. trachurus* and *S. japonicus* showed a lower frequency of occurrence. In terms of abundance, the most important species was *B. boops*, followed by the blennies and *P. acarne* (Table 2). Both the

Table 1 Diet composition of the predator (*Dicentrarchus labrax*)

Taxa	<i>N%</i>	<i>W%</i>	<i>FO</i>	<i>Q</i>	<i>IRI</i>
Crustacea					
Amphipoda	1.43	0.00	2.33	0.00	3.32
<i>Necora puber</i>	2.86	0.87	4.65	2.48	17.33
<i>Polybius henslowi</i>	44.29	48.25	18.60	2136.66	1721.54
Total	48.57	49.12	25.58	2385.61	2498.97
Gastropoda					
Unidentified	2.86	2.73	4.65	7.81	26.00
Osteichthyes					
<i>Boops boops</i>	24.29	19.33	37.21	469.34	1622.76
Blenniidae	5.71	0.25	2.33	1.42	13.87
<i>Pagellus acarne</i>	4.29	7.10	6.98	30.44	79.46
<i>Scomber japonicus</i>	10.00	19.30	6.25	192.98	183.11
<i>Trachurus trachurus</i>	2.86	2.17	6.98	6.19	35.05
Total	47.14	48.14	67.44	2269.51	6426.13
Algae					
Unidentified	1.43	0.01	2.33	1.42	3.35

%N numeric percentage, *%W* weight percentage, *FO* frequency of occurrence, *Q* feeding coefficient, *IRI* index of relative importance

Table 2 General information regarding the predator (*Dicentrarchus labrax*) and reef fish preys

	FO	Abundance ^c		ML ^c (cm)	L-1st-Mat	M (%)	Juvenile ^c (%)	Predation (%)	E
		Mean	Max						
<i>Dicentrarchus labrax</i>	86	55 ± 24	264	40 ± 3	38.5 (Farrugio and Le Corre 1986)		56		
<i>Boops boops</i>	100	499 ± 367	1,266	6 ± 3	15.7 (Monteiro et al. 2006)	4–35 ^b	99.7	73	+0.38(0.20)
<i>Pagellus acarne</i>	54	74 ± 16	388	10 ± 2	21 (Santos et al. 1995b)	7–48 ^a	100	43	+0.29(0.36)
<i>Scomber japonicus</i>	25	46 ± 92	269	21 ± 3	31 (Anon. Unpublished)	13–40 ^a	100	50	+0.09(0.10)
<i>Trachurus trachurus</i>	29	54 ± 101	318	12 ± 2	22 (Borges and Gordo unpublished)	25–36 ^a	100	75	−0.07(0.03)
Blenniidae	100	76 ± 21	678	6 ± 2	–	–	–	9	−0.18
Total prey	–	749 ± 493	2242	–	–	7–25 ^b	–	90	

FO frequency of occurrence; Mean (± standard deviation) and maximum (Max) species abundance (no. of individuals per reef), ML mean total length, L-1st Mat size at first maturity (reference between brackets), M range of prey percentage mortality, Juvenile percentage of juveniles, Predation percentage of times *D. labrax* forage upon available preys, E Ivlev electivity index (standard deviation)

^a Based on the range of monthly mean mortality estimations (just for demersal reef associated species)

^b Based on regression analysis (just for demersal reef associated species)

^c Based on visual census

mean and maximum length of all demersal reef fish species found in sea bass stomach were below their size at first maturity (Table 2).

Predator–prey abundance variation

The monthly variations in abundance of sea bass and reef fish prey found in bass stomachs are shown in Fig. 2. High abundances of *D. labrax* per reef set occur between December and February. High densities of *B. boops* were found in May and August, with low values in February and March. High densities of *P. acarne* were observed in April and May. *T. trachurus* was only observed between February and June, with high abundances recorded in May and June. *S. japonicus* was recorded in April and later again between July and September when abundance was high. High overall prey abundances were recorded between April and May (2004) and the lowest between January and March (2004). The mean number of total prey available was 749 individuals per reef set (Table 2).

Predator–prey relationships

The highest abundances of *D. labrax* were recorded when the total abundance of preys was below their mean abundance value (Fig. 2; Table 2). In contrast, the highest total prey values were recorded from April to July when the numbers of sea bass were below the mean. Relationships between prey–predator abundance showed negative correlations between *D. labrax* abundance and both *B. boops* ($r = -0.6$; $P = 0.03$; $df = 13$) and *P. acarne* ($r = -0.5$; $P = 0.09$; $df = 6$). Negative correlations between *D. labrax*

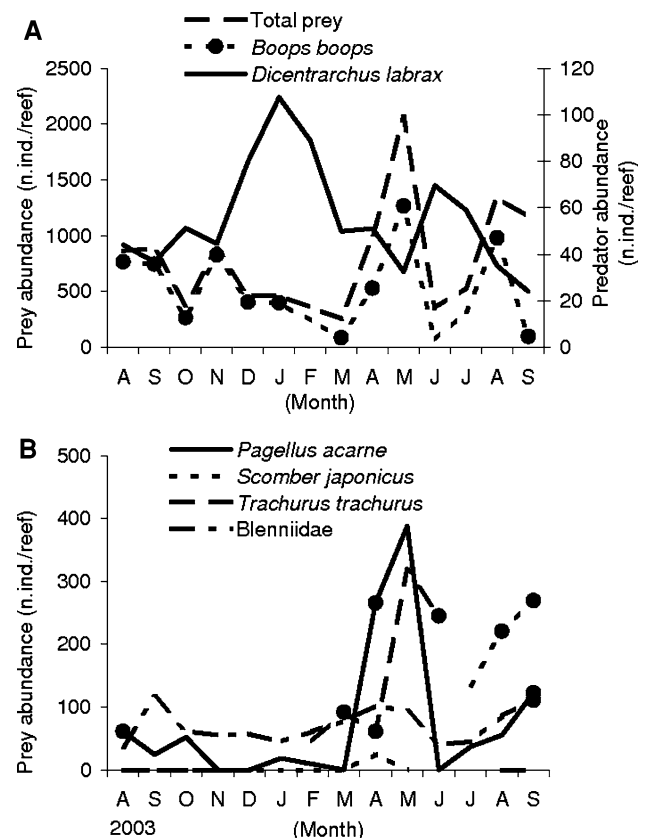


Fig. 2 a Monthly density variation of *D. labrax* (predator), *B. boops* (principal prey) and overall reef fish preys. b Mean abundance of the other prey species (*P. acarne*, *S. japonicus*, *T. trachurus* and Blenniidae). Filled circle represent the presence of a given prey in sea bass stomachs in a given month

abundances and both the latter prey species abundance suggests that predation affects prey abundance (Hypothesis I). However, correlations between sea bass and both *S. scomber*

($r = -0.3$; $P = 0.33$; $df = 3$) and *T. trachurus* ($r = 0.1$; $P = 0.77$; $df = 4$) were not statistically significant. Nevertheless, a strong negative correlation was observed ($r = -0.6$; $P = 0.03$; $df = 13$) between sea bass and total reef prey species abundance, suggesting that sea bass predation significantly affects the abundance of AR demersal prey.

The relationship between the number of each prey species per sea bass stomach and prey abundance (Hypothesis II) is shown in Fig. 3. There was a significant relationship between consumption and abundance (or availability) of *B. boops* ($P = 0.04$; $df = 10$) and *T. trachurus* ($R^2_{T. trachurus} = 0.56$, $P_{T. trachurus} = 0.02$; $df = 3$). For *S. japonicus* ($R^2_{S. japonicus} = 0.42$, $P_{S. japonicus} = 0.15$; $df = 3$) and *P. acarne* ($R^2_{P. acarne} = 0.05$, $P_{P. acarne} = 0.9$; $df = 6$) the relationships were not significant. A significant positive relationship between consumption and overall prey abundance was found ($P = 0.01$; $df = 10$; Fig. 3b). These results suggest that for Hypothesis II, the null hypothesis can be rejected and we can conclude that there is a relationship between prey abundance and predation by sea bass on the artificial reefs.

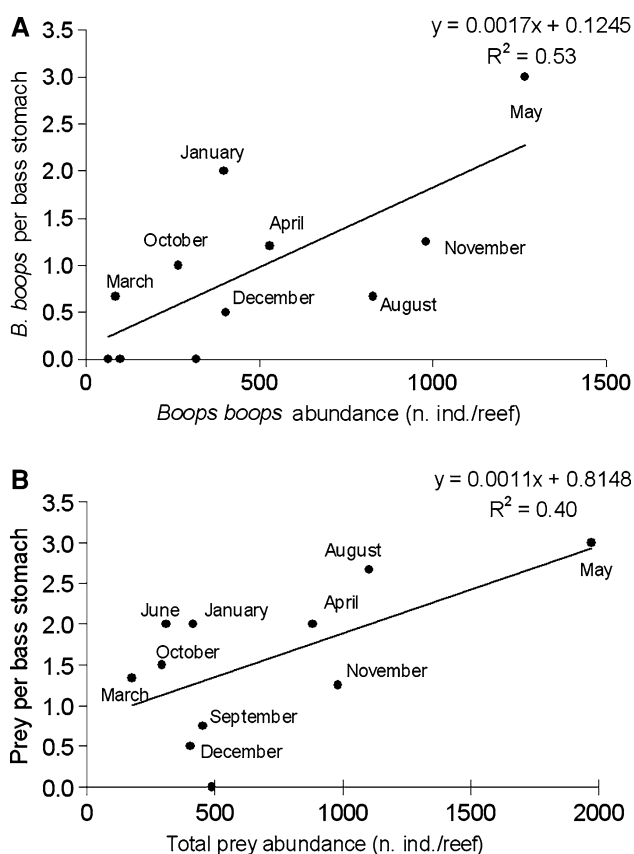


Fig. 3 Predator–prey relationship between the numbers of individuals (**a** for *B. boops* and **b** for total demersal reef fish associated prey species) found per sea bass stomach as a function of prey abundance on the reef

Independently of the monthly availability of prey abundance (Fig. 2), the predation on reef fish species occurred every month, with the exception of July when all reef fish prey species were absent from the bass diet. However, in the latter month the overall abundance of fish reef species was very low (Fig. 2). Nonetheless, overall predation occurred 90% of the times that both sea bass and prey species were simultaneously observed in the AR (Table 2; Fig. 2). Predation was high for *T. trachurus* (75%) and *B. boops* (73%), but lower for *S. japonicus* (50%) and *P. acarne* (43%) (Table 2). It is worth noting that although several AR fish species were available to *D. labrax*, it preferentially fed on *B. boops*, which was the only prey species that was always available on the ARs (Table 2). Indeed, despite other prey species being available in the AR, they were not always eaten by the sea bass (e.g. *P. acarne* in January, May and June). In November and December, although *S. japonicus* was not observed in the AR, it was found in the bass stomachs.

A positive relationship (Hypothesis III) was found between *B. boops* mortality and bass abundance ($P = 0.07$; $df = 10$, Fig. 4a). For the remaining species, the relationships were not significant. Nevertheless, a strong significant positive relationship ($P = 0.03$; $df = 10$) was also found between predator abundance and overall prey mortality (Fig. 4b). Therefore, we reject the null hypothesis and accept that predation abundance affects prey mortality. Prey mortality depends on bass abundance. For instance, the highest number of preys available was recorded in May but mortality was low as bass abundance was low. In April, bass abundance was high and consequently mortality increased (Figs. 3, 4). Overall demersal prey mortality varied between 7 and 25%. However, the maximum mortality value was high ($\geq 35\%$) for all prey species (Table 2). In June, mortality was exclusively of *T. trachurus* (36%) that was the most abundant species. In October, mortality was exclusively of *P. acarne* (48%).

Ivlev's electivity index denotes high positive electivity values for *B. boops*, indicating bass prey selective preference (exclusive selection) on the latter species (Table 2). The Ivlev electivity index was also positive for *P. acarne*. However, deviance values for *P. acarne* and *S. scomber* allow the predator to be categorized as being both selective and with no preference for these species (Table 2). The electivity values and associated deviance *T. trachurus*, suggested little or no bass preference for this species. The electivity value was negative in the case of the blennies, meaning that bass as no preference on this resident reef fish group. Considering Ivlev's electivity index, and respective associated deviances, it is possible to state that the feeding preference of sea bass is affected by the available abundance of demersal reef species, such as the *B. boops* and *P. acarne* that were the reef fish species that contributed most

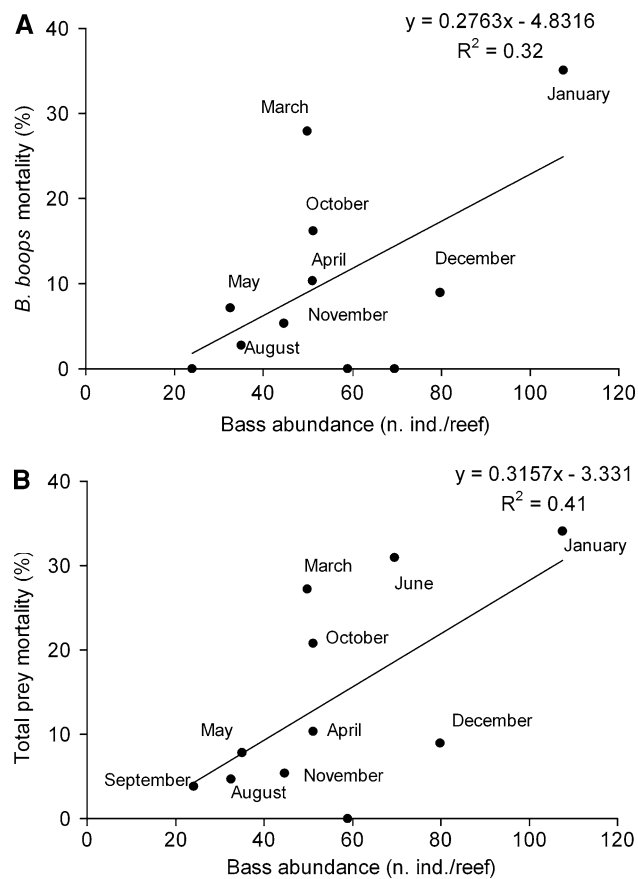


Fig. 4 Prey percent mortality (M%), for *B. boops* (a) and for all demersal (b) reef fish associated prey species, as a function of the number of predators

to the *D. labrax* diet. Considering Ivlev's index (Table 2) and both Q and IRI (Table 1) for hypothesis VI, the tentative conclusion is that the bass is selective. However, this preference was strongly affected by the abundance of the available prey (see Hypothesis II).

Discussion

The effect of predation by piscivores in AR fish assemblages is poorly known. Nonetheless, in coral reef areas (Hixon and Bettes 1993; Hixon and Jones 2005), rocky intertidal (Sih et al. 1985; Connell 2002; Johnson 2006) and freshwater systems (Zaret 1980), it has been shown that predation can have a significant effect on the distribution and abundance of prey fish species within a community. Our study showed that *D. labrax*, a transient predator, feeds on juvenile demersal species, such as *B. boops*, *T. trachurus*, *P. acarne* and *S. japonicus*, which are attracted to the ARs. These species are among the most abundant in ARs (Santos 1997; Santos et al. 2005). Moreover, they occasionally also feed on some resident

fish species (belonging to the Blenniidae family) and hard reef macrobenthic species such as *N. puber*, a common species in Algarve ARs (Leitão et al. 2007). Other studies also found several finfish species (*D. labrax* (cannibalism), *Pomatoschistus* spp., *Sprattus sprattus*, *Atherina boyeri*) and a variety of macrozoobenthos species in the sea bass diet (<http://www.fishbase.org>). In the present study, demersal reef fish prey species were found in the stomach of sea bass in almost all months and in addition, predation on total reef fish prey items occurred 90% of the time. It seems that the sea bass is a very opportunistic species that takes advantage of the overwhelming concentration/aggregation of small fish attracted to ARs. The number of empty stomachs was low, with the prey digestion level indicating that feeding activity was recent, probably during the early morning hours.

The idea that fish predation is strongly influenced by prey abundance is highlighted in many studies (Hixon and Carr 1997; Stewart and Jones 2001; Connell 2002). Connell (2000) discovered that larger schools of fish suffer greater rates of mortality, a direct challenge to the idea of safety-in-numbers. A similar phenomenon may also occur in the Algarve ARs with sea bass predation on juvenile (0^+ and 1^+ age classes) demersal reef species, especially on those that were recorded in high abundances and frequency of occurrence, such as *B. boops* and *P. acarne*. Carr and Hixon (1995) observed that the low survivorship (40–80%) of new recruits on reefs where resident predators had been removed might be due to transient predators (e.g. jacks, Carangidae). The influence of predation on early juveniles of commercially valuable species, such as sea bass, was observed to cause density-dependent mortality (Laffaille et al. 2000). In fact, in our study a negative correlation was found between total demersal AR prey abundance and the sea bass numbers, suggesting that predation can influence prey abundance (Hypothesis I). Moreover, the mean numbers of prey per sea bass stomach increased with the demersal reef fish prey abundance (Hypothesis II) and higher predator density caused higher mortality of demersal reef fish associated species (Hypothesis III).

Understanding natural causes of density dependence is essential for identifying possible sources of population regulation (Hixon 1991). Hixon and Beets (1993) found that reef-associated piscivores do not always control the number of co-occurring fish prey, but rather set the upper limit to the number of fish prey that occupy a reef. On some reefs, where predator numbers were high, the latter authors showed that average abundance of prey decreases over time as predators increase. Moreover, in the same study the authors reported that there was a clear negative correlation between predator numbers and prey abundance. Nevertheless, they considered these relationships causal and explained the results by the rapid consumption of recruited

cohorts on reefs by resident piscivores, with predation occasionally directly observed. Herrera et al. (2002) observed that some piscivore species were chiefly responsible for controlling AR fish productivity. The authors report that the seasonal arrival of dense schools of small pelagic species seems to attract piscivores from the sandy bottom biotope with 1–2 months' time lag.

The hypothetical estimates of mortality bridge the conceptual link between density and loss of prey at varying predator density. The issue of whether predator aggregation is strong enough to cause proportionally greater predator-driven declines, as prey abundance increase, is fundamental to the concept of artificial habitats fish assemblage regulation. The results showed that prey consumption was dependent on prey abundance and that mortality increase with bass abundance. Predators often account for a large fraction of mortality (e.g. Carr and Hixon 1995; Connell 1997; Hixon and Carr 1997; Forrester and Steele 2000) and predator impacts can be reduced by habitat manipulations that increase the availability of shelter for prey or reduce prey encounter rates with predators (Anderson 2001, and references therein; Forrester and Steele 2004; Overholtzer-McLeod 2006).

The deployment of ARs in the Algarve may contribute to an increase in the natural mortality of juvenile, or young of the year, demersal reef prey associated species by facilitating predator–prey interactions. In this study, prey mortality varied between 4 and 48% and may be particularly high ($\geq 35\%$) for all prey species. When properly designed, located and constructed, with an adequate quantity of stable and durable substrate, man-made reefs can, in theory, be equally as productive as naturally occurring hard-bottom habitats, limited only by the lifespan of the materials utilized. Given the material used in the construction of the Algarve ARs, the structures in place could favour prey–predator encounters for the next several hundred years. Given the large number of ARs in Algarve waters (588 AR sets, 20,580 units), constituting the largest complex of this type in European waters, the predation of bass on aggregations of juveniles could have a cumulative effect on local prey populations, especially those with high frequency of occurrence, abundance and that suffer higher mortalities on AR (e.g. *B. boops*). Thomas (1974) showed that fishes decrease the linear distance travelled after successfully discovering food and increased it after rejecting a food item. This behaviour facilitates avoiding the unproductive foraging areas, increasing the changes of discovering productive areas, and remaining in the proximity of discovered food. Optimal foraging theory (reviewed by Krebs 1978; Hart 1986) could also be applied to movements of bass between reefs. Predators are predicted to distribute themselves and to move between reefs so as to maximize net energy gain. Therefore fishes should

distribute between reefs according to reef profitability. Theories of “marginal value” (Hart 1986) and “giving up time” (Krebs 1978) predict that predators should leave a reef when the energy yield from food resources is reduced to a certain level. Foragers should spend more time at reefs with abundant food resources than at reefs with low food availability.

The results showed that predation was the primary cause of density-related mortality. Nevertheless, prey mortalities vary considerably according to bass density. Rather than density-dependence, “density-vague regulation” (Sale and Tolimieri 2000; Strong 1986) may be more useful for explaining bass predation/mortality on ARs. The “density-vague” approach to population regulation recognizes that the influence of density is weak if present over a broad range of densities and that variation within this range is caused by other factors (Strong 1986).

Some AR species were not always present in the bass diet. This may be related to predator's feeding preference. Indeed, although prey selection was strongly affected by the abundance of some prey (*B. boops*) our results (Hypothesis IV) suggest that the bass is selective. Nevertheless, for less frequent and abundant prey the variability in Ivlev's index allows bass to be categorized as either selective or with no preference (*P. acarne*; *S. japonicus*) or exclusive avoidance and no preference (*T. trachurus*). This means that in the presence of several fish prey species, bass feed preferentially on the more abundant prey species. The concept of accessibility (Ivlev 1961) or vulnerability (Lewis and Helms 1964) of prey has important implications for understanding resource utilization by predators. Lewis and Helms (1964) proposed that the vulnerability of the prey was more important than morphological and behavioural characteristics of the predator, while Diggins et al. (1979), suggest that both prey density and vulnerability are of importance in predator selection. Ivlev's electivity index denoted positive electivity for *B. boops* and *P. acarne*, no preference for *S. japonicus* and *T. trachurus* and almost a complete avoidance for blennies. The Algarve AR sets are composed of open cubic concrete reef modules of low complexity/heterogeneity that provide relatively few refuges for blennies. Nevertheless, they are not very vulnerable to bass as they take refuge in the concavities (authors' personal observation) provided by the AR macrobenthic community (e.g. dead oyster shells, bryozoans, etc.).

Hixon and Beets (1993) established refuge from predation as an important function of reef fish structure. Bayle-Sempere et al. (2001) showed that the small number of recruits in large volume ARs might be associated to predation by larger fishes, since predators have a greater ability to capture prey in low structural complexity artificial habitats. Indeed, juveniles of the demersal species such

as *B. boops* and *P. acarne*, that are highly vulnerable to sea bass predation, do not use ARs to avoid predation. However, it is worth noting that for hypothesis II and III significant results were observed only for the total prey community and/or *B. boops*. This suggests that while bass respond to overall prey density, they select (Hypothesis IV) the most available and vulnerable species.

The Faro/Ancão AR system covers an area of 12.21 km², at a depth range of 17–24 m, in a 36-km² zone, where natural reefs are scarce (only 2.7 km²). This AR system located off Faro and the Ria Formosa lagoon was designed to provide suitable hard structure habitat for juveniles that seasonally migrate from the lagoon to coastal waters as reported by Monteiro et al. (1990). Thus, in addition to the high capacity of man made structures to attract/aggregate fish, the Faro/Ancão reef fish assemblages may be strongly influenced by the input of large numbers of fish migrating from the Ria Formosa to the AR, favouring the local increase of prey. This may contribute to creating optimal foraging areas for bass. High levels of bass predation on juveniles at these sites may affect the transfer of stock from the lagoon to the adjacent coastal waters. Several authors report that predation is affected by the abundance of available prey (Hixon and Carr 1997; Stewart and Jones 2001; Connell 2002). Therefore, predation rate and consequently effects on reef species may be higher on ARs that are associated with the annual recruitment of juveniles from nearby nurseries. However, this is not the case for the juvenile fish species found in the sea bass stomachs, which are very common in Algarve coastal waters but not particularly abundant in the Ria Formosa lagoon.

At present, there are not enough data to prove that sea bass predation rates are higher in ARs located near nursery grounds or whether predation is similar throughout the Algarve AR complex, which occupies an area of 43 km² within a coastline of approximately 110 km. However, as both predator and prey species are very common on the southern coast of the Algarve, it is expected that this *D. labrax*-prey interaction occurs along all the local ARs. Density-dependent predation can occur on patchy habitats because predators disproportionately forage in patches of high relative to low prey density (Hixon and Carr 1997; Stewart and Jones 2001). Spatially density-dependent predation may be common in some reef settings, particularly on isolated patches (such as those off the Algarve), and less common or important on continuous reefs (Sandin and Pacala 2005). Overholtzer-McLeod (2006) showed that mortality was density dependent on coral reef patches that were spatially isolated (separated by 50 m) and density independent on reef patches that were aggregated (separated by 5 m). The sea bass, a transient and opportunistic open-water species, can easily pursue their prey throughout

the AR structures. The Algarve AR organization was designed to act as a “chain net” so that fish can move from one reef set to the other (~70 m) and/or between reef groups (~300 m). The presence of *D. labrax* in the ARs has been particularly noted in the last 3 years, a period which coincided with the enlargement of the Faro/Ancão AR system during 2003 (Francisco Leitão, unpublished data). Because of the durability of AR material (concrete), we can predict a continuous long-term predation effect of sea bass on reef fish assemblages. Hueckel and Buckley (1987) found that as an AR increases in age, food resources and predator populations associated with the reef also increase. Moreover, as greater numbers of ARs are deployed, the probability of prey–predator encounters increases and consequently, fish prey become more vulnerable to predation.

D. labrax predation has contributed to the decrease of the abundance of prey demersal species on the ARs. Whether this decrease results in lower catches or recruitment of prey species to the fishery, either locally or in an adjacent region, depends on stock dynamics. If the prey species are migratory, which is not the case here, then heavy predation mortality in one region will probably result in lower levels of recruitment/abundance (exploitable biomass) in the adjacent areas. By attracting and aggregating juvenile fish, ARs create feeding areas for predators. Therefore, heavy AR mortality due to predation occurring along Algarve ARs could reduce recruitment of prey species to the local small-scale fisheries. Caley (1993) showed that predators may affect community structure of older age classes through time-lagged effects on the survivorship of younger age classes and that a greater number of species of recruit and resident fishes were more abundant on reefs from which predators had been removed. On the other hand, while the juvenile prey species are too small to be caught by hook or net gear, they provide food for the sea bass, an economically very important species for inshore artisanal and recreational fisheries. Increases in catches of predators, such as the sea bass, in the vicinity of ARs is a consequence of their attraction to ARs due to the feeding opportunities provided by higher prey concentrations. However, due to their economic value, such a “bait” effect, may lead to an increase in vulnerability of predators to local fisheries, as suggested by Polovina (1991).

The present study suggests that it is necessary to consider ecological effects such as predator–prey interactions, prior to the development of artificial habitats as a tool for habitat rehabilitation. The effects of predator–prey interactions, particularly in the vicinity of artificial bottom habitats, on fish resources are poorly understood, complex and require in-depth study. Both short and long-term effects of sea bass predation on the Algarve AR reef fish assemblage are difficult to monitor due to the constant

evolution of these ecosystems. If fish attraction from surrounding areas is rapid, then long-term, cumulative and indirect effects due to fishing and predation (or both), become difficult to infer.

Spatial associations (or lack thereof) between predator and prey density will, however, be species and context-specific. In some situations, the density of predatory fish does covary with prey density (Stewart and Jones 2001), and an aggregative response is the putative cause of density-dependent mortality in other reef fishes (Hixon and Carr 1997; Anderson 2001). Our ability to assess the nature and effects of density-dependent interactions on population dynamics should thus be improved by work that identifies the underlying biological interactions causing density-dependent mortality, and characterizes the spatial and temporal domains at which those interactions operate (Forrester and Steele 2004; Overholtzer-McLeod 2006).

The results obtained in this study highlight the importance of defining a suitable strategy to manage these artificial habitats. Therefore, understanding inter-specific interactions (e.g. predator–prey) is important for conservation and management and for evaluating the long-term effects of reef deployment, especially in areas where nearby lagoons supply juvenile fish to the adjacent coastal waters.

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