

## LETTER

# Compartments in a marine food web associated with phylogeny, body mass, and habitat structure

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## Abstract

A long-standing question in community ecology is whether food webs are organized in compartments, where species within the same compartment interact frequently among themselves, but show fewer interactions with species from other compartments. Finding evidence for this community organization is important since compartmentalization may strongly affect food web robustness to perturbation. However, few studies have found unequivocal evidence of compartments, and none has quantified the suite of mechanisms generating such a structure. Here, we combine computational tools from the physics of complex networks with phylogenetic statistical methods to show that a large marine food web is organized in compartments, and that body size, phylogeny, and spatial structure are jointly associated with such a compartmentalized structure. Sharks account for the majority of predatory interactions within their compartments. Phylogenetically closely related shark species tend to occupy different compartments and have divergent trophic levels, suggesting that competition may play an important role structuring some of these compartments. Current overfishing of sharks has the potential to change the structural properties, which might eventually affect the stability of the food web.

## Keywords

Compartments, complex networks, food web, phylogenetic analyses, sharks, trophic level.

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## INTRODUCTION

Food webs are representations of who eats whom in ecological communities. Understanding how these webs are structured, and which factors underlie such a structure, are major goals in ecology with far-reaching consequences for the conservation of species-rich communities. A long-held tenet in ecology has been to determine whether food webs are structured in compartments, i.e. subgroups of highly interacting species with little interaction between the subgroups (Paine 1963, 1980; Cohen 1978; Pimm & Lawton 1980; Sugihara 1983; Raffaelli & Hall 1992; Krause *et al.* 2003; Melián & Bascompte 2004). This search was spurred by the belief that compartmentalization greatly affects food web stability (May 1972; Pimm 1979; Pimm & Lawton 1980; Solow *et al.* 1999). For example, a compartmentalized structure may reduce the propagation of a perturbation through the entire food web (Melián & Bascompte 2002). This is particularly relevant for marine ecosystems because they are currently under intense fishing pressures (Pauly

*et al.* 1998; Myers & Worm 2003), and have the potential for community-wide cascading effects (Carpenter & Kitchell 1993; Bascompte *et al.* 2005; Mumby *et al.* 2007; Myers *et al.* 2007).

In spite of all this interest, however, there are few unequivocal examples of compartmentalization in food webs (e.g. Girvan & Newman 2002; Krause *et al.* 2003; see Olesen *et al.* 2007 for plant-animal mutualistic interactions), and even less mechanistic explanations for such compartments. Habitat boundaries were first suggested as the most likely explanation of compartments (Pimm & Lawton 1980), and more recent papers have found evidence for such a factor (Girvan & Newman 2002; Krause *et al.* 2003). Body size (Paine 1963; Cohen *et al.* 1993, 2003; Williams & Martinez 2000; Emmerson & Raffaelli 2004; Stouffer *et al.* 2005; Petchey *et al.* 2008) and evolutionary history (Cattin *et al.* 2004) have also been adduced to be an important explanation for food web structure. Therefore, new studies are necessary to disentangle the role of these factors in shaping the architecture of food webs. These studies should

also consider the role of phylogeny as a determinant of community structure (Webb *et al.* 2002), because phenotypic attributes such as body mass, relative abundance, and trophic level may be partly determined by species evolutionary history (Blomberg *et al.* 2003; Garland *et al.* 2005).

Here, we (i) detect compartments in a real, large marine food web; (ii) test if body size, habitat structure, and phylogeny are associated to such a compartmentalized structure; and (iii) analyse the disproportionate importance of sharks in shaping these compartments. To do so, we combine recently developed computational tools to analyse complex networks (Newman & Girvan 2004; Guimerà & Amaral 2005) with phylogenetic statistical tools (Blomberg *et al.* 2003; Garland *et al.* 2005). Our results suggest that past evolutionary history of the species involved can be very important in explaining current community patterns (Cattin *et al.* 2004; Rezende *et al.* 2007).

## MATERIALS AND METHODS

### The food web

We analysed a Caribbean marine food web depicting a total of 3313 trophic interactions between 249 species/trophic groups (Opitz 1996; Bascompte *et al.* 2005). This food web encompasses all benthic and pelagic communities from the surface to a 100-m depth in an area of *c.* 1000 km<sup>2</sup>, and includes detritus, 3 primary producer groups, 35 invertebrate taxa, 208 fish species, sea turtles and sea birds (see Dataset S1 for the food web with its constituent species and interactions). We also used additional information on species presence/absence across five habitat types, which provides a crude estimate of spatial structure in this marine ecosystem (Melián *et al.* 2005): mangrove/estuaries, coral reefs, sea-grass beds/algal mats, sand, and off-shore reefs. Details on how the food web was assembled, on habitat characteristics and on the data strengths and limitations (particularly in relation to the analysis of gut contents), are discussed elsewhere (Bascompte *et al.* 2005; Melián *et al.* 2005).

Analyses of network structure were performed with the totality of the food web. Employing information on species biomass, body mass, metabolic rates, and diet composition (Bascompte *et al.* 2005), we calculated the strength of a predator–prey interaction as:

$$(Q/B)_j \times DC_{ij}, \quad (1)$$

where  $(Q/B)_j$  is the number of times an age-structured population of predator *j* consumes its own weight per day, and  $DC_{ij}$  is the proportion of prey *i* in the diet of predator *j* estimated from stomach content analysis. Thus, our resulting matrix describes the absolute magnitude of biomass flowing from each prey to each predator per unit time

(Berlow *et al.* 2004). Note that the measure in eqn 1 is equivalent to the one used by Bascompte *et al.* (2005), but without dividing by prey biomass. This is because here we are interested in a property of the predator species, namely the biomass flowing from a prey to its predator, while Bascompte *et al.* (2005) focused in the per capita effects of predators on their prey, which is directly dependent on the prey biomass.

### Network structure and trophic levels

We first addressed if the food web was significantly subdivided into different compartments in relation to random expectation. We used a module-finding algorithm (Newman & Girvan 2004) combined with a simulated annealing optimization approach (Guimerà & Amaral 2005) to detect food web compartments. Specifically, we have used the simplest generalization to weighted networks of the modularity implemented in the Guimerà and Amaral's algorithm (Guimerà & Amaral 2005; Guimerà *et al.* 2007). Basically, the program employs a heuristic procedure to find an optimal solution for the maximization of a function called modularity (Newman & Girvan 2004). For weighted networks, where  $w_{ij}$  represents the weight of the interaction between predator *j* and prey *i*, the modularity is given by (see Guimerà *et al.* 2007):

$$M_W(P) = \sum_{s=1}^{N_M} \left[ \left( \frac{w_s^{\text{in}}}{W} \right) - \left( \frac{w_s^{\text{all}}}{2W} \right)^2 \right], \quad (2)$$

where  $W = \sum_{i \geq j} w_{ij}$  is the sum of the weights of all predator–prey interactions across the entire network,  $w_s^{\text{in}}$  is the sum of the weights of the links  $w_{ij}$  within compartment *s*, and  $w_s^{\text{all}} = \sum_{i \in s} \sum_j w_{ij}$  is the sum of the weights of the interactions involving species *i* within module *s* with all other species.

This function maximizes the weights of links between nodes belonging to the same compartment and minimizes the weight of links between nodes belonging to different compartments. A network with high modularity is such that the density of links (and their weights) inside compartments is significantly higher than the random expectation for such a density. Because values of interaction strength spanned six orders of magnitude, we ranked interaction strengths from 1 to 6 according to their order of magnitude (note that these ranks reflect the flux of biomass from prey to predators on a log-scale). From these analyses, we obtained the value of modularity for the food web, the number and identity of compartments detected by the algorithm, and the role of each species in the web. We estimated how well connected each species is to the other species inside the compartment ( $\bar{z}$ -score or standardized within-compartment degree,  $\bar{z}$ ), and how well the interactions of a species are distributed among different compartments (participation coefficient, *PC*, vary-

ing between 0 and 1). The role of each species in the web can be described with these two indices. For instance, species with high  $\alpha$  and low  $PC$  are well connected only within their compartments; species with low  $\alpha$  and high  $PC$  act primarily as connectors between compartments; and species with both high  $\alpha$  and  $PC$  are network hubs, i.e. well connected both within and across compartments (details in Guimerà & Amaral 2005).

We also calculated the trophic level of each species/taxon in the food web, employing the positional index  $d$  (Bersier *et al.* 2002). This index takes into account the amount of biomass that comes to a species from its prey, and how much biomass flows from this species to its predators, varying between 0 and 1: basal species that do not predate any other species on the web have a  $d = 0$ , top predators have a  $d = 1$ , and intermediate species that act as both prey and predators have a  $d$  between 0 and 1. Because we were interested primarily on the interactions between fish species, we excluded other taxa on the food web prior to calculations of  $d$ .

### The phylogeny

We assembled a fish phylogeny (Fig. S1) encompassing 116 species employing multiple sources from the literature (Text in Supporting Information). This corresponds to 46.6% of all nodes in the web or 55.8% of the fish species. These species are involved in 2307 trophic links, corresponding to 69.6% of the total number of interactions. Visual inspection of the data and preliminary analyses suggested that this subset of species was an accurate representation of the food web (no biases were observed when comparing results obtained with the entire dataset against analyses including only species with available phylogenetic information). Our composite phylogeny was based primarily on the supertree of Mank *et al.* (2005), whereas phylogenetic relations between species at lower levels were based on different molecular studies (Text in Supporting Information). Conflicting branching patterns were resolved conservatively and kept as soft polytomies. Major groups that could not be confidently placed in the tree were not included (e.g. Serranidae, Pomacanthidae, Pomacentridae, and Sciaenidae). Divergence times were not available for all clades, hence we employed Ornstein–Uhlenbeck (OU) transformations to obtain adequate branch lengths for phylogenetic analyses (Blomberg *et al.* 2003). We selected the branch lengths that would best fit the distribution of body mass in our sample, because the distribution of body mass often matches a simple stochastic model of character evolution (Blomberg *et al.* 2003). Starting from three different arbitrary branch lengths with different levels of hierarchy (Nee, Grafen, and Pagel in PDTree; Garland *et al.* 1992), we first obtained the best fitting tree for each case employing maximum likelihood methods and subsequently selected the

branch lengths that best explained the covariance of body mass across species (i.e. lowest Mean squared error (MSE); Blomberg *et al.* 2003).

### Statistical analyses

Analyses encompassed the following procedures: (i) discriminant analyses to assess which ecological and phenotypic variables could significantly discriminate different compartments; (ii) phylogenetic analyses to determine whether these variables were partly explained by phylogeny; (iii) ANCOVA testing for prey selection among predators of different compartments; (iv) randomization to determine if competition between shark species from different compartments is lower than that expected from random sampling.

#### *Discriminant function analyses*

Discriminant analyses were performed separately for each variable (five 0–1 habitat categories coding for absence/presence of each species in each of the five habitat types, trophic level, log-transformed body mass and relative abundance), to diagnose which phenotypic attributes could underlie the compartmentalization of the food web.

#### *Phylogenetic effects*

We employed two complementary approaches to estimate how phylogeny affected trophic level, body mass, and habitat (the relevant traits associated with food web structure as judged by discriminant analyses; see Results). First, we compared goodness of fit of ordinary least-square regression models (OLS) with phylogenetically generalized regression models (PGLS). Whereas OLS assumes no hierarchical structure in the data, the correlations between residuals in the PGLS models vary depending on the degree of relatedness between species, accounting for phylogenetic effects (Garland *et al.* 2005). We compared the Akaike's information criterion (AIC) values across models as indicators of the models' goodness of fit, using the smaller-is-better formulation (as a rule of thumb, models whose AIC is  $\leq 2$  units larger than the best fit model also have substantial support, whereas those with models resulting in AIC values  $> 10$  units larger have virtually no support). Regression models included trophic level as the dependent variable and body mass and habitat as the independent variables (comparisons between sharks and other fish species were also performed by including a 0–1 variable in these models), and were performed with the Matlab program Regressionv2.m (Lavin *et al.* 2008).

Second, we employed randomization tests to determine whether the phenotypic data had significant phylogenetic signal (i.e. the tendency of closely related species to have similar phenotypes; Blomberg *et al.* 2003; Garland *et al.* 2005). These analyses were primarily performed to estimate

if phylogenetic effects in food web structure exist (see also Ives & Godfray 2006; Rezende *et al.* 2007). Subsequent comparisons did not control for phylogeny because the structure of the food web is inherently determined by the identity of the species in the community.

#### *Prey selection*

To determine whether predators from different compartments select prey of contrasting sizes, we performed an ANCOVA comparing mass of prey consumed by different predators weighting by the strength of each interaction. These comparisons encompassed 205 fish species (invertebrates were not included because estimates of size were not available), and pairwise differences between compartments were estimated with a posteriori Tukey test. All prey were included in this analysis (including those belonging to other compartments), and interactions were weighted employing the rank from 1 to 6 used to estimate compartmentalization. This analysis is more refined and has a higher statistical power than the discriminant analysis described before because it discriminates between predators and prey within each compartment. As a complementary analysis, we employed a logistic regression to test for size effects at the interaction level. Specifically, we assessed whether the relation between predator and prey sizes differs across predatory interactions within compartments vs. interactions between compartments. Significance of the predator by prey size interaction in the logistic regression was tested employing the Wald coefficient, which follows a chi-squared distribution.

#### *Competition between shark species*

Subsequently, we explored if competition between shark species was associated with the compartmentalized structure of the food web. Competition was estimated employing the Jaccard index of similarity from qualitative interaction matrices. The similarity between two predator species,  $i$  and  $j$ , was defined as  $S(i, j) = a/(a + b + c)$ , where  $a$ ,  $b$ , and  $c$  represent the number of shared prey species, the number of prey exclusive to predator  $i$ , and the number exclusive to predator  $j$ , respectively. This resulted in a matrix of pairwise competitive interactions between species within a single compartment (31 interactions) or involving species in different compartments (74 interactions), with their respective average competitions,  $S1$  and  $S2$ . We tested if this classification was able to discriminate between regions of high and low competition with a randomization procedure: sharks were shuffled across compartments 1000 times to generate a random distribution of  $S1$ . The null hypothesis was rejected if  $S1$  in the real matrix was higher than 95% of the randomizations ( $\alpha = 0.05$ ). This would suggest that competition is significantly higher between species in the same compartment and lower between species belonging to different compartments than expected from random sampling.

## RESULTS

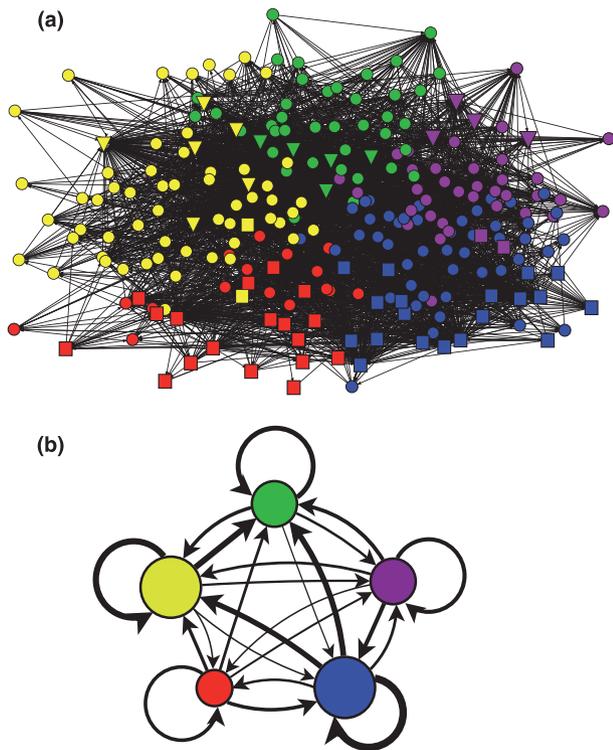
### Network structure

The Caribbean food web presented a significantly compartmentalized structure. Its average modularity level was  $0.212 \pm 0.001$  SD ( $n = 100$  replicates of the simulated annealing algorithm). Hence, the number of predator–prey interactions within each of the assigned compartments is roughly 21% higher than that expected from a network with the same compartments but random interactions between species. To assess the significance of this compartmentalized structure controlling for each species' number of interactions, we compared the previous modularity level with that corresponding to 100 randomizations of the food web preserving the number of interactions per species. The modularity of this population of randomizations was  $0.1672 \pm 0.002$  SD, significantly lower than for the real food web ( $P < 0.01$ ).

Our subsequent analyses of the Caribbean food web are based on the output of a randomly chosen replicate of the simulated annealing algorithm. This replicate indicated a division of the food web into five distinct compartments (colour-coded in Fig. 1). To assess if this replicate was a representative sample for subsequent analyses and to quantify the consistency of results across replicates, we first checked how the number of compartments varied across replicates. There was no variation across the 100 replicates, i.e. simulated annealing always ended up in detecting five compartments. Then, we quantified how conserved the distribution of species within compartments was across replicates. We calculated, for a given pair of species observed in the same compartment in the working replicate, how often that particular pair of species was also found within the same compartment in the remaining 99 replicates. Coincident results represented 78% of the cases. Hence, nearly 4 out of 5 pairs of species fell consistently within the same compartments across replicates of the simulated annealing algorithm running on the real food web. Among sharks, results were even more robust, with coincident results corresponding to 83% of the cases. Of the 15 shark species in the food web, only 2 species were not consistently assigned to the same compartment across replicates. When these species are removed, coincident results increase to 99.6% of the times. This is a strong indication of the robustness of our classification of the food web in compartments, particularly with regards to shark species.

### Determinants of compartmentalization

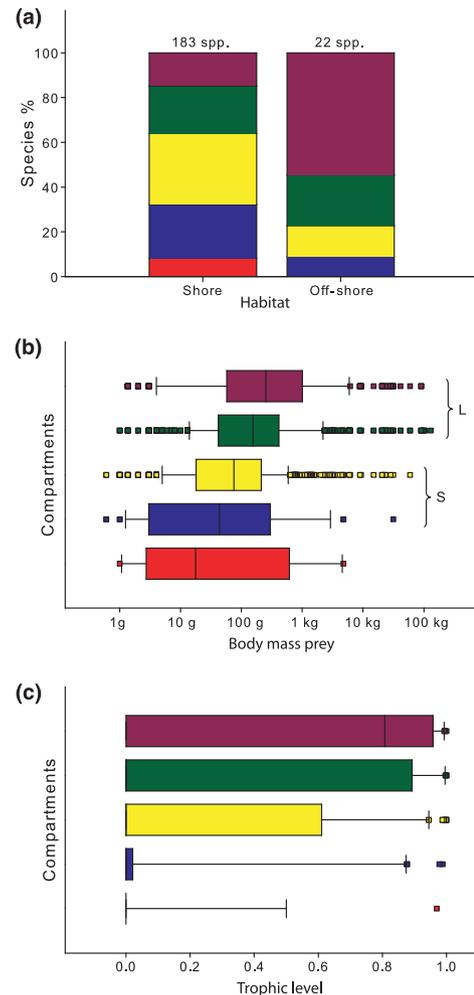
Discriminant analyses suggested that body mass, trophic level, and habitat (0–1 coding for species inhabiting in-shore or off-shore) can significantly discriminate between compartments ( $F_{4,200} > 4.37$ ,  $P \leq 0.002$  in all cases). However,



**Figure 1** Compartmentalized structure of the Caribbean food web. (a) The entire food web. Nodes of different colours represent species belonging to different compartments, whereas each link represents a predator-prey interaction. Squares, circles, and triangles indicate non-fish, bony fish, and shark species, respectively. (b) Schematic diagram of the compartmentalized structure of the food web. Each node represents a compartment and arrows indicate the flow of biomass from the prey to predator within (loops) and between compartments. The size of each node is proportional to the number of species in that compartment. The thickness of the arrows indicates the fraction of the interactions between these two compartments in relation to the total for the food web.

only trophic level remained significant when these three factors were included in the model, suggesting that differences between compartments in trophic level, body size, and habitat fell within a single discriminant axis. Comparisons of discriminant canonical functions estimated at group means suggested that trophic level and habitat can discriminate the purple compartment from the remaining ones (Fig. 2). Habitat can also discriminate the red compartment, but canonical functions cannot be calculated in this case because all species from this compartment inhabit in-shore (Fig. 2).

These discriminant analyses did not discern between predators and prey within each compartment, hence we also



**Figure 2** Effects of habitat and body size across compartments. (a) Relative frequency of species belonging to different compartments in shore vs. off-shore habitats. (b) Range of prey size consumed by predators from different compartments. There was a clear dichotomy between compartments where predators eat large prey (*L*) and compartments where predators consume smaller prey (*S*): pairwise comparisons were statistically significant across (Tukey's  $P < 0.001$  in four pairwise comparisons) but not within ( $P > 0.14$  in two pairwise comparisons) these groups. Results of comparisons with the red group were not included in the figure for clarity; it encompassed just a few predatory interactions and only differed significantly from the purple compartment ( $P = 0.033$ ). (c) Trophic level of species in each compartment, ranging between 0 (species with no fish prey) and 1 (species with no fish predators). The median (line within the box), 25th and 75th percentiles (box), 10th and 90th percentiles (error bars), and outliers are shown in boxplots (b) and (c).

analysed whether predators from different compartments selected prey of different sizes. Results from logistic regressions showed that the interaction between predator and prey body mass significantly explains whether predation

occurs within or between compartments ( $\chi^2 = 5.4$ , 1 d.f.,  $P = 0.02$ ), and supported that predatory interactions between species of similar body size occur significantly more often within compartments. This suggests that predation on different prey sizes contributes to the compartmentalization of the food web. Accordingly, predators of different compartments consumed prey of significantly different size, according to a regular ANOVA weighed by interaction strength ( $F_{4,1948} = 23.9$ ,  $P < 0.0001$ ). A subsequent Tukey test showed that pairwise differences between compartments were significant in some instances ( $P < 0.001$ ), and separated two compartments where predators consume larger prey (green and purple) from two other compartments where predators eat smaller prey (yellow and blue; Fig. 2). A similar analysis showed that prey size differences were more dramatic across sharks (yellow, green, and purple compartments). Prey consumed by sharks from different compartments differed significantly in size ( $F_{2,1298} = 68.3$ ,  $P < 0.0001$ ), and pairwise comparisons were always statistically significant (Tukey's  $P < 0.0001$  in all cases). In summary, these analyses suggest that the compartmentalized structure of the food web is associated with interspecific differences in trophic level, habitat, and body size.

### Phylogenetic effects

The association between body size and habitat with trophic level was significant in most OLS and PGLS regressions (Table 1), hence these variables are correlated as suggested by the discriminant analysis. Comparisons between different models suggested that phylogenetic effects can be very important in our dataset because PGLS models performed considerably better than OLS regressions (differences between values of the AIC from OLS models and their PGLS counterpart were always higher than 50; Table 1). Interestingly, habitat effects were significant or bordered significance in OLS but not in PGLS models (Table 1),

suggesting that habitat distribution is also phylogenetically structured. Randomization analyses support this conclusion: habitat, body mass, relative abundance, and trophic level exhibited significant phylogenetic signal ( $P < 0.001$  in all cases; Table S1).

Phylogenetic effects were pervasive in this dataset but contrastingly different between sharks and bony fishes. Whereas compartments encompassed closely phylogenetically related species of bony fishes ( $P < 0.05$  in three of the five compartments), the opposite pattern was observed in sharks (Fig. 3). Trophic levels among sharks showed significant phylogenetic overdispersion (i.e. closely related species tended to differ more than expected at random; Blomberg *et al.* 2003; Helmus *et al.* 2007) when analyses were performed for this group alone ( $P = 0.023$ ; Fig. 3). That is, closely related shark species tended to be segregated in different compartments so that sharks within each compartment were less related to each other than expected if they were picked at random. Interestingly, randomization results suggested that competitive interactions were significantly lower than expected by chance when they involved species in different compartments ( $P < 0.008$ ; Fig. 4), suggesting that compartmentalization decreases competition between shark species.

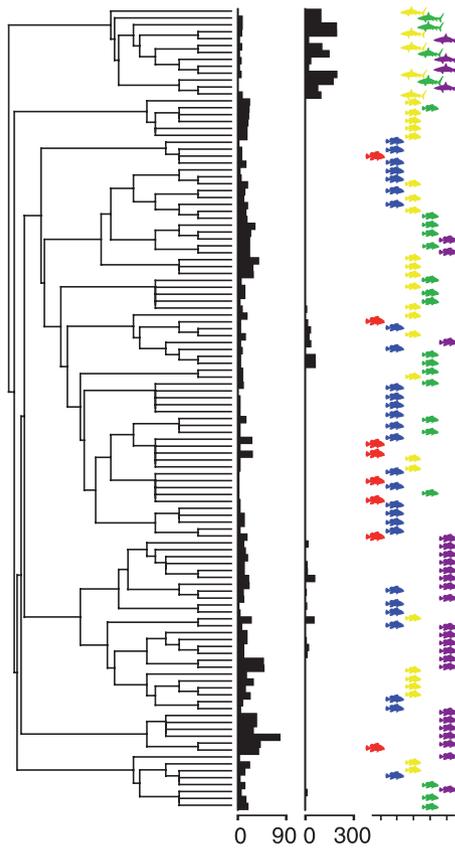
Sharks also differed from other fishes in several aspects. For instance, sharks were significantly larger and occupied higher trophic levels than other fishes ( $F_{1,114} = 10.80$ ,  $P = 0.001$  and  $F_{1,114} = 4.84$ ,  $P = 0.030$ , respectively). Although body mass was a significant predictor of trophic level (Table 1), the difference in trophic level between sharks and other fishes remained significant after controlling for habitat and body mass ( $F_{1,112} = 2.85$ , one-tailed  $P = 0.047$ ; Table 1). Furthermore, their number of predatory interactions was higher than those of other fish species after controlling for body mass ( $F_{1,113} = 45.0$ ,  $P < 0.001$ ). Because sharks are opportunistic generalist feeders, it is possible that their prominent role in the food web partly stems from characteristic foraging mode and feeding

**Table 1** Comparison between different ordinary (OLS) and phylogenetic regression models (PGLS) testing for the effects of habitat, body mass, and taxonomic affiliation (bony fishes vs. sharks) on trophic levels

Model	Regression	AIC	Habitat	Mass	Taxa
Habitat	OLS	131.18	$F_{1,114} = 10.01^{**}$		
	PGLS	36.97	$F_{1,114} = 0.01$		
Habitat + mass	OLS	96.57	$F_{1,113} = 3.15$	$F_{1,113} = 41.94^{***}$	
	PGLS	28.63	$F_{1,113} = 0.37$	$F_{1,113} = 10.53^{**}$	
Habitat + mass + taxa	OLS	86.27	$F_{1,112} = 2.32$	$F_{1,112} = 12.36^{***}$	$F_{1,112} = 12.52^{***}$
	PGLS†	27.71	$F_{1,112} = 0.40$	$F_{1,112} = 7.09^{**}$	$F_{1,112} = 2.85$

\*\*Two-tailed  $P < 0.01$ , \*\*\* $P < 0.001$ .

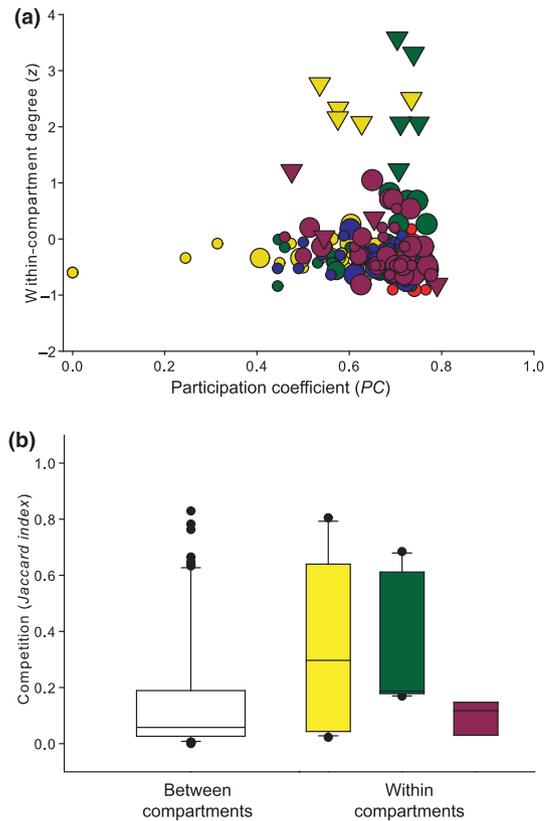
†Model with best fit according to smaller-is-better AIC criterion. AIC, Akaike information criterion.



**Figure 3** Fish phylogeny employed for phylogenetic statistical analyses, showing also species-specific ecological traits and compartment identity. Histograms show how frequently each species is a prey (left) and a predator (right) in the food web, estimated as the total number of interactions weighed by their strength (see Materials and methods).

strategies. In our dataset, sharks predated upon species with a significantly broader range of sizes than other fish species of similar size, according to PGLS controlling for body size ( $F_{1,41} = 4.0$ , one-tailed  $P = 0.026$ ; species with trophic level = 0 were excluded from this analysis).

Sharks account for a disproportionately large fraction of the predations in the food web (Fig. 3), hence we also analysed their contribution to food web structure. The role of each species in the network can be described by a combination of its standardized within-compartment degree ( $\bar{z}$ ), and its  $PC$ . While  $\bar{z}$  measures how well connected one species is to another in its compartment,  $PC$  indicates how well distributed the interactions of a species are among different compartments (see Methods). Whereas the  $PC$  did not differ significantly between sharks and bony fishes (mean  $0.65 \pm 0.01$  SE across all species; ANCOVA,  $F_{1,114} = 0.01$ ,  $P = 0.90$ ), the standardized within-compartment degree was significantly higher in sharks (ANCOVA,  $F_{1,114} = 192.2$ ,  $P < 0.001$ ; Fig. 4). Neither  $PC$  nor  $\bar{z}$  was



**Figure 4** (a) Role of each species within the food web. Each symbol describes the participation coefficient and the within-compartment degree of each fish species. Symbol size is proportional to trophic level. Species are colour-coded according to the compartment to which they belong. Triangles and circles represent sharks and bony fishes, respectively. (b) Mean competition between shark species across and within compartments. Randomization analyses show that pairwise competition is significantly lower between species belonging to different compartments.

significantly associated with body mass ( $P > 0.65$  in both cases). Therefore, the importance of sharks for network structure stems primarily from their higher total number of interactions.

## DISCUSSION

Although the existence of compartments and their role for food web stability have been debated for more than three decades, there are very few unequivocal examples of compartmentalization (e.g. Girvan & Newman 2002; Krause *et al.* 2003). More importantly, despite early suggestion of the potential role of habitat boundaries (Pimm & Lawton 1980; Girvan & Newman 2002; Krause *et al.* 2003), almost no study has clearly identified the mechanisms behind a compartmentalized structure. In this paper, not only do we describe

compartments in a large marine food web, but also assess their association with several ecological and evolutionary variables. Specifically, here we provide the first empirical evidence that body size mediating predator–prey associations (Paine 1963; Cohen *et al.* 1993, 2003; Emmerson & Raffaelli 2004) can be associated to a compartmentalized food web. This is particularly remarkable considering that we worked with species averages, hence effects were strong enough to be detected despite considerable measurement noise (e.g. intra-specific variation in size during development should affect species' potential preys and predators). Additional factors such as diet specialization and spatial structure also contribute to this compartmentalized organization.

This food web has a comparatively high number of species and interactions, a high resolution (the bulk of nodes correspond to taxonomic species), and quantitative information. However, some caveats about this dataset should be made explicit, such as a high variability in diets and biomass estimates, an unequal level of resolution, and potential effects of anthropogenic impact. The first issue arises from the limitation of the samples of stomach contents. While the stomach contents of all fish species in the food web were obtained from the exhaustive analysis by Randall (1967), the number of sampled individuals per species was highly variable, with 54 species represented only by 10 or less individuals. Still, Randall's (1967) attempts to minimize biases are considerable, focusing only on stomach contents to control for differences in digestibility across prey items and making an effort to collect individuals across all habitats. Therefore, despite the small sample size in a few cases, the samples were as representative as possible.

The second potential limitation of this food web is its unequal level of resolution across all taxa. While fishes are all resolved to the species level, there is some degree of lumping for zooplankton, microfauna, sponges, octopuses, echinuroids, and other invertebrates. It is very difficult to assess to what extent results may be affected by this biased level of resolution (except that the food web would become larger and more complex). Nonetheless, it is worth noting that most of the invertebrates fall within two compartments (red and blue; Fig. 1). The remaining network, composed primarily of fishes with a more homogeneous level of resolution, also presents a compartmentalized structure, which apparently results from the feeding choices of sharks.

With regards to anthropogenic impact, the whole Caribbean ecosystem has been largely overfished in the last decades with profound implications for its structure and functioning (Jackson 1997). It is very difficult to assess to what extent the structure reported here reflects the pristine organization of the community or a transient stage along a destructive process, and future work is necessary in this context (e.g. Randall's dataset has been assembled over four decades ago, hence more up-to-date records may help elucidating the

community-wide effects of continuous overfishing). In summary, this study employs one of the most comprehensive datasets to analyse the evolutionary and ecological correlates underlying food web structure, with the caveat that potential limitations associated with this dataset should always be kept in mind (for a detailed account of the strengths and limitations of this dataset, see the Supporting Material in Bascompte *et al.* 2005).

Results suggest that phylogenetic effects are important determinants of community structure, in part because body size and habitat were significantly associated with evolutionary history. Phylogenetic analyses also point towards the unique role of some groups of species in the food web. Our analyses show that a few shark species account for a significantly large fraction of the predatory interactions within compartments (Figs 3 and 4). Although body size partly accounts for the role of sharks as top predators and organizers of compartments, differences in foraging mode probably account for the size-independent differences in trophic levels and number of predatory interactions between sharks and other fishes. To our knowledge, this is the first time that phylogeny is shown to correlate with food web structure. This complements the dominant concept of body size as a driver of food web structure and imposes controlling for phylogeny before any test on the role of body size. Our results support recent work emphasizing that while a model of optimal foraging and allometric considerations predicts 65% of trophic links, an accurate prediction of food web structure will require incorporation of traits other than body size (Petchey *et al.* 2008). Our paper builds on that by identifying additional factors such as past evolutionary history and habitat structure.

Previous studies have suggested that compartmentalization may increase network stability (May 1972; Krause *et al.* 2003; Teng & McCann 2004; however, see Pimm 1979). Besides its relation to stability *sensu strictu*, it would be interesting to address how a compartmentalized structure could reduce competition between closely related species and thus facilitate community biodiversity, as seems to be the case with sharks (Paine 1980; Duffy *et al.* 2007). Significant phylogenetic overdispersion among sharks suggests that closely related species tend to occupy different compartments, emphasizing how phylogenetic information can shed light on the evolutionary basis of community structure (see also Webb *et al.* 2002). Accordingly, competition was significantly higher between shark species in the same compartment. Although this result, together with the observed phylogenetic overdispersion, suggests that niche displacement between top predators might partly explain the compartmentalized structure, it is unclear if these patterns have resulted from ongoing competition or reflect competitive exclusion that has occurred in the past (or the interaction between both). Regardless of the ultimate determinants of these patterns, it is

clear that closely related shark species tend to occupy different compartments, and this pattern might partly explain the coexistence of these species in the community.

To sum up, our results suggest that the Caribbean food web is organized in compartments that correlate with habitat and dietary preferences (prey size). They also illustrate how network and phylogenetic analyses can shed light on the ecological and evolutionary mechanisms underlying community structure (Helmus *et al.* 2007), providing circumstantial evidence that competition and niche displacement at higher trophic levels might be associated with the compartmentalized structure of the food web. These observations give rise to testable predictions that may provide important insights on the relation between species composition, species richness, and community stability. For instance, future studies may address whether modularity across food webs is positively related with interspecific variation in body size or phylogenetic diversity, and determine how consistently competition and niche displacement between predators high in the food chain can be associated with compartmentalization. From a conservation perspective, our results highlight the importance of sharks for the compartmentalized organization, hence potentially for the stability and biodiversity of the Caribbean food web. Selective fishing of predators can have cascading effects across the entire ecosystem (Daskalov *et al.* 2007) and this might be particularly true for sharks in this community (see also Bascompte *et al.* 2005). Our findings add to these previous results by showing that the overfishing of a few species of sharks may jeopardize the structural properties of the entire food web and its derived stability. In this context, it is worth noting that the role of sharks in the community is partly determined by their evolutionary history, and not a mere reflection of their larger body sizes.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Dataset S1** Excel file describing food web.

**Figure S1** *Phylogeny*: Phylogenetic hypothesis employed in this study.

**Table S1** *Phylogenetic signal*: Testing for the presence of phylogenetic signal in species phenotypic attributes, employing the MatLab program PHYSIG.M (14).

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