

NOTA:

REEF FISH FORAGING ASSOCIATIONS AT MALPELO ISLAND, COLOMBIA (TROPICAL EASTERN PACIFIC)

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RESUMEN

Asociaciones alimentarias en peces arrecifales en isla Malpelo, Colombia (Pacífico Oriental Tropical). Varias especies de animales marinos establecen temporalmente asociaciones de caza interespecíficas, en las cuales especies oportunistas siguen a otras especies llamadas nucleares mientras estas buscan alimento pues disturban el sustrato. Este tipo de comportamiento ha sido observado entre algunas especies de peces arrecifales en la isla Malpelo en el Pacífico colombiano. La morena *Gymnothorax dovii* y el jurel *Caranx melampygus* fueron identificados como especies nucleares mientras cazaban dentro del sitio conocido como El Arrecife. Estas especies fueron acompañadas por algunos meros *Dermatolepis dermatolepis* y *Mycteroperca olfax*, jurel *Seriola rivoliana*, pez corneta *Aulostomus chinensis*, la vieja *Bodianus diplotaenia* y en algunas ocasiones por el jurel *Caranx melampygus*, que tuvo ambos comportamientos (nuclear/seguidor). Este tipo de interacción alimentaria es un importante componente en la estructura trófica de las comunidades arrecifales que ocurren en todos los mares.

PALABRAS CLAVES: Asociación alimentaria, nucleares-seguidores, depredación, Colombia.

Several studies have reported temporary interspecific feeding associations between different species of reef fishes and, less often, other animals (e.g. Hobson, 1968; Lukoschek and McCormick, 2000; Sazima *et al.*, 2007). These associations usually occur when food-seeking animals called “nuclear species” disturb the substrate, thus attracting opportunistic species or “followers” (Fricke, 1975; Fishelson, 1977; Krajewski, 2009). It has been suggested that followers are also attracted by particular characteristics of nuclear species such as body shape, size, color, and swimming behaviour (Fricke, 1975; Fishelson, 1977; Bshary *et al.*, 2006;

Araújo *et al.*, 2009; Krajewski, 2009). The nuclear role is mostly played by fishes, and less often by octopuses, sea-stars, and turtles (Diamant and Shpigel, 1985; Gibran, 2002; Sazima *et al.*, 2004; Pereira *et al.*, 2011), while the follower role may be played by several opportunistic animals, mostly fishes (Bellwood *et al.*, 2006).

Multi-species fish foraging associations range from simple to complex, and from highly transient to obligate associations (Sazima *et al.*, 2007). They are formed by a wide range of fish species, from many families, and include most trophic groups (Lukoschek and McCormick, 2000; Pereira *et al.*, 2012). Most nuclear reef fish species are active hunters (e.g. carnivores such as eels, groupers, or stingrays) and occasionally herbivores (such as acanthurids and labrids; Ormond, 1980; Lukoschek and McCormick, 2000; Sazima *et al.*, 2005). Species considered as followers are carnivores (especially zoobenthivores) with opportunistic foraging behaviours, a common feature in reef fishes (Strand, 1988; Lukoschek and McCormick, 2000), which would explain the greater number of follower species compared to that of the nuclear ones (Gerking, 1994; Sazima *et al.*, 2005; Bellwood *et al.*, 2006).

These associations are facilitated by carnivorous fishes employing a variety of foraging tactics including disguise, ambush, stalking, and roving (Sazima, 1986; Gerking, 1994; Krajewski, 2009). Some species usually use one or two tactics, whereas others may employ several tactics according to circumstances (Hobson, 1968; Gerking, 1994). Due to the great behavioural plasticity found in reef fishes, many species could play both the nuclear and the follower role. For example, at a single location species of the Mullidae, Labridae, Lutjanidae, Serranidae, Balistidae, and Muraenidae can play both roles (Fricke, 1975; Ormond, 1980; Aronson and Sanderson, 1987; Strand, 1988; Sazima *et al.*, 2007; Pereira *et al.*, 2011).

Despite the nuclear-follower feeding interactions being a common interspecific interaction among reef fishes, little is known about the number of species and individuals that participate in a given feeding association event. Indeed, most studies focused on one or a few nuclear and/or follower species or even a particular kind of association (Ormond, 1980; Diamant and Shpigel, 1985; Strand, 1988; Baird, 1993; Auster and Lindholm, 2002; Gerhardinger *et al.*, 2006; Félix and Hackradt, 2008).

We describe here an interspecific foraging association between several individuals of two nuclear species, the moray eel *Gymnothorax dovii* (Muraenidae) and the jack *Caranx melampygus* (Carangidae) with numerous individuals of several follower species: the groupers *Dermatolepis dermatolepis* and *Mycteroperca olfax* (Serranidae), the trumpetfish *Aulostomus chinensis* (Aulostomidae), the hogfish *Bodianus diplotaenia* (Labridae), and the jacks *Seriola rivoliana* and *Caranx melampygus* (Carangidae) (Table 1).

Table 1. Fish species recorded in foraging associations at Malpelo Island, Colombia, Eastern Tropical Pacific, between February 2002 and August 2009. Sites, depths, hours (indicated to the nearest 15 min), species involved, number of individuals, and the nuclear or follower role each species played in each recorded association are indicated.

| Site | Depth (m) | Hour | Species | Number of individuals | Role |
|--------------------|-----------|-------|----------------------------------|-----------------------|----------|
| El Arrecife | 26 | 12:30 | <i>Caranx melampygus</i> | 40 | Nuclear |
| | 26 | 12:30 | <i>Dermatolepis dermatolepis</i> | 20 | Follower |
| | 26 | 12:30 | <i>Gymnothorax dovii</i> | 12 | Follower |
| Bajo de Junior | 25 | 08:00 | <i>Caranx melampygus</i> | 30 | Nuclear |
| | 25 | 08:00 | <i>Dermatolepis dermatolepis</i> | 15 | Follower |
| | 25 | 08:00 | <i>Gymnothorax dovii</i> | 4 | Follower |
| El Arrecife | 15 | 16:00 | <i>Caranx melampygus</i> | 50 | Nuclear |
| | 15 | 16:00 | <i>Dermatolepis dermatolepis</i> | 80 | Follower |
| | 15 | 16:00 | <i>Gymnothorax dovii</i> | 8 | Follower |
| | 15 | 16:00 | <i>Mycteroperca olfax</i> | 1 | Follower |
| Bajo del Monstruo | 13 | 07:30 | <i>Gymnothorax dovii</i> | 4 | Nuclear |
| | 13 | 07:30 | <i>Caranx melampygus</i> | 20 | Follower |
| | 13 | 07:30 | <i>Dermatolepis dermatolepis</i> | 40 | Follower |
| El Arrecife | 18 | 12:00 | <i>Gymnothorax dovii</i> | 6 | Nuclear |
| | 18 | 12:00 | <i>Caranx melampygus</i> | 50 | Follower |
| | 18 | 12:00 | <i>Dermatolepis dermatolepis</i> | 70 | Follower |
| | 18 | 12:00 | <i>Aulostomus chinensis</i> | 1 | Follower |
| | 18 | 12:00 | <i>Mycteroperca olfax</i> | 1 | Follower |
| La Nevera | 15 | 16:45 | <i>Gymnothorax dovii</i> | 20 | Nuclear |
| | 15 | 16:45 | <i>Dermatolepis dermatolepis</i> | 80 | Follower |
| | 15 | 16:45 | <i>Caranx melampygus</i> | 6 | Follower |
| | 15 | 16:45 | <i>Mycteroperca olfax</i> | 2 | Follower |
| El Arrecife | 20 | 07:30 | <i>Gymnothorax dovii</i> | 10 | Nuclear |
| | 20 | 07:30 | <i>Seriola rivoliana</i> | 15 | Follower |
| | 20 | 07:30 | <i>Caranx melampygus</i> | 50 | Follower |
| | 20 | 07:30 | <i>Dermatolepis dermatolepis</i> | 50 | Follower |
| La Nevera | 20 | 08:00 | <i>Caranx melampygus</i> | 15 | Nuclear |
| | 20 | 08:00 | <i>Dermatolepis dermatolepis</i> | 60 | Follower |
| El Arrecife | 22 | 15:30 | <i>Gymnothorax dovii</i> | 7 | Nuclear |
| | 22 | 15:30 | <i>Caranx melampygus</i> | 15 | Follower |
| | 22 | 15:30 | <i>Dermatolepis dermatolepis</i> | 30 | Follower |
| | 22 | 15:30 | <i>Mycteroperca olfax</i> | 2 | Follower |
| Pared del Náufrago | 26 | 09:00 | <i>Gymnothorax dovii</i> | 5 | Nuclear |
| | 26 | 09:00 | <i>Caranx melampygus</i> | 40 | Follower |
| | 26 | 09:00 | <i>Dermatolepis dermatolepis</i> | 70 | Follower |
| | 26 | 09:00 | <i>Seriola rivoliana</i> | 4 | Follower |
| El Arrecife | 20 | 09:10 | <i>Caranx melampygus</i> | 40 | Nuclear |
| | 20 | 09:10 | <i>Dermatolepis dermatolepis</i> | 60 | Follower |
| | 20 | 09:10 | <i>Seriola rivoliana</i> | 1 | Follower |
| El Arrecife | 23 | 11:30 | <i>Gymnothorax dovii</i> | 20 | Nuclear |
| | 23 | 11:30 | <i>Caranx melampygus</i> | 40 | Follower |

Continuation Table 1

| Site | Depth (m) | Hour | Species | Number of individuals | Role |
|-------------|-----------|-------|----------------------------------|-----------------------|----------|
| | 23 | 11:30 | <i>Dermatolepis dermatolepis</i> | 60 | Follower |
| | 23 | 11:30 | <i>Mycteroperca olfax</i> | 3 | Follower |
| El Arrecife | 12 | 09:30 | <i>Gymnothorax dovii</i> | 20 | Nuclear |
| | 12 | 09:30 | <i>Dermatolepis dermatolepis</i> | 50 | Follower |
| | 12 | 09:30 | <i>Mycteroperca olfax</i> | 1 | Follower |
| | 12 | 09:30 | <i>Aulostomus chinensis</i> | 2 | Follower |
| | 12 | 09:30 | <i>Caranx melampygus</i> | 12 | Follower |
| El Arrecife | 17 | 15:30 | <i>Gymnothorax dovii</i> | 18 | Nuclear |
| | 17 | 15:30 | <i>Caranx melampygus</i> | 12 | Follower |
| | 17 | 15:30 | <i>Dermatolepis dermatolepis</i> | 45 | Follower |
| | 17 | 15:30 | <i>Caranx melampygus</i> | 30 | Follower |
| | 17 | 15:30 | <i>Mycteroperca olfax</i> | 18 | Follower |
| El Arrecife | 21 | 11:00 | <i>Gymnothorax dovii</i> | 7 | Nuclear |
| | 21 | 11:00 | <i>Bodianus diplotaenia</i> | 1 | Follower |
| | 21 | 11:00 | <i>Caranx melampygus</i> | 12 | Follower |
| | 21 | 11:00 | <i>Bodianus diplotaenia</i> | 2 | Follower |
| | 21 | 11:00 | <i>Dermatolepis dermatolepis</i> | 20 | Follower |
| El Arrecife | 10 | 15:30 | <i>Gymnothorax dovii</i> | 5 | Nuclear |
| | 10 | 15:30 | <i>Caranx melampygus</i> | 7 | Follower |
| | 10 | 15:30 | <i>Dermatolepis dermatolepis</i> | 40 | Follower |
| El Arrecife | 12 | 15:00 | <i>Gymnothorax dovii</i> | 15 | Nuclear |
| | 12 | 15:00 | <i>Bodianus diplotaenia</i> | 2 | Follower |
| | 12 | 15:00 | <i>Caranx melampygus</i> | 1 | Follower |
| | 12 | 15:00 | <i>Dermatolepis dermatolepis</i> | 30 | Follower |
| | 12 | 15:00 | <i>Aulostomus chinensis</i> | 1 | Follower |
| | 12 | 15:00 | <i>Seriola rivoliana</i> | 1 | Follower |
| El Arrecife | 21 | 08:00 | <i>Gymnothorax dovii</i> | 10 | Nuclear |
| | 21 | 08:00 | <i>Aulostomus chinensis</i> | 1 | Follower |
| | 21 | 08:00 | <i>Dermatolepis dermatolepis</i> | 25 | Follower |
| El Arrecife | 15 | 10:00 | <i>Gymnothorax dovii</i> | 20 | Nuclear |
| | 15 | 10:00 | <i>Caranx melampygus</i> | 25 | Follower |
| | 15 | 10:00 | <i>Mycteroperca olfax</i> | 2 | Follower |
| | 15 | 10:00 | <i>Dermatolepis dermatolepis</i> | 50 | Follower |
| | 15 | 10:00 | <i>Bodianus diplotaenia</i> | 1 | Follower |

Observations were made at Malpelo Island (4°00'05"N, 81°36'30"W), a Sanctuary of Marine Fauna and Flora located 380 km off the coast of Colombia, in the Tropical Eastern Pacific (Birkeland *et al.*, 1975; Zapata and Vargas-Ángel, 2003). The island is characterized by a rocky bottom and a relatively high cover of underdeveloped coral formations (Birkeland *et al.*, 1975; Zapata and Vargas-Ángel, 2003). The nuclear-follower feeding interactions were recorded by scuba divers on

19 occasions between February 2002 and August 2009, and between 08:00-16:00 h at depths ranging from 8 to 27 m (Table 1). Nuclear-follower association was most commonly observed at a site known as El Arrecife (Figure 1). The interactions are described based on observations and photographs taken during fish visual censuses on the reef.

Feeding associations were initiated by the foraging activity of the moray eel *Gymnothorax dovii* (74% of the records) or the jack *Caranx melampygus* (26% of the records). The moray poked into coral branches (*Pocillopora* spp.) or entered within reef crevices in search of prey. This behaviour caused small fishes

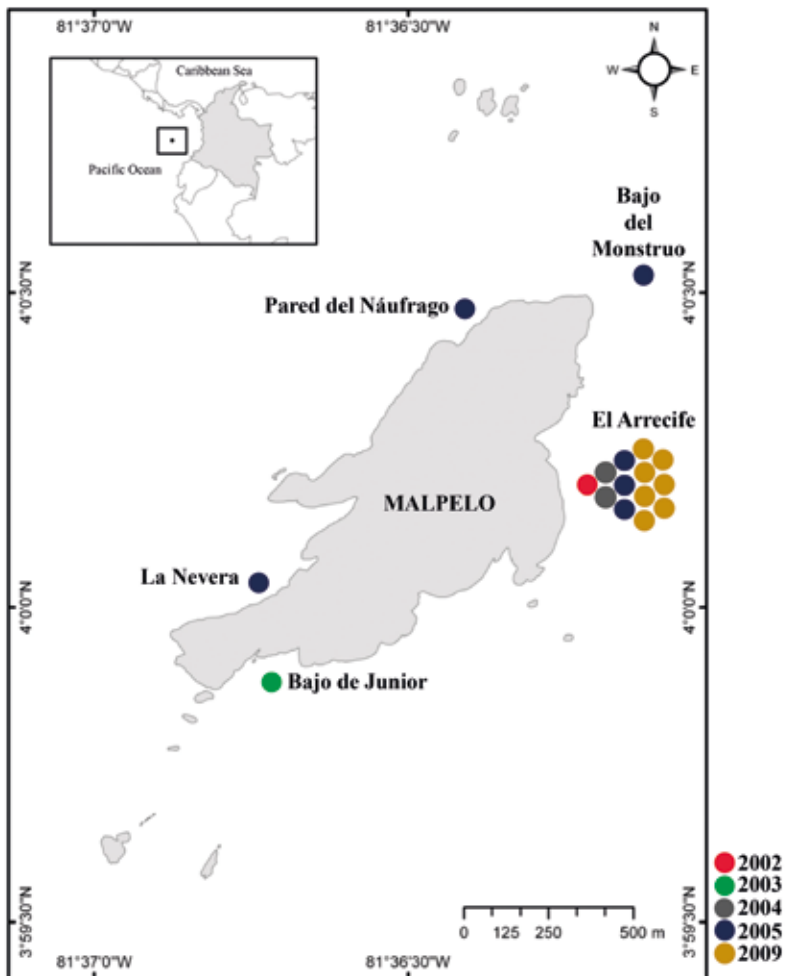


Figure 1. Map and location of foraging associations observed around a year at Malpelo Island, Colombia. Colors are different years (see on the right of the square).

and invertebrates to flee and move out from their hiding places, thus attracting nearby carnivorous fishes such as groupers, jacks, and hogfish. These opportunistic predators fed frantically on the fishes and invertebrates as the latter fled from their hideouts (Figure 2). The grouper *Dermatolepis dermatolepis* took part as a follower in all recorded interactions, whereas the jack *C. melampygu* was the second most important follower, although sometimes it also played the role of nuclear species (Table 1). *Caranx melampygu* swam in groups and circled the reef portion that was under the moray's inspection, this behaviour possibly attracted other species such as groupers and trumpetfish.

The number of morays that took part in the interspecific foraging association varied (4-20), while the number of follower fishes was generally > 60 individuals, mostly groupers, jacks, trumpetfish, and hogfish, although there were instances that involved up to six different fish species (Table 1). The duration of a foraging bout at a single site varied from 3 to 5 min, after which the nuclear species would move, followed by the other predators until arriving at a new site where another feeding bout would begin (Figure 3). This process was repeated for an unknown, but presumably limited, number of times as the group of nuclear species and their followers moved along the reef.

This study stands out as the first record of a large feeding aggregation in the Eastern Tropical Pacific, as the association contained several individuals of two nuclear species and many individuals of at least four follower species. A nuclear-follower fish foraging association involving a moray eel and two species of groupers is known from the Gulf of California, but the recorded number of participants is only up to four individuals (Craig and Erisman, 2010). Other studies have described the behaviour of adult *D. dermatolepis* and *Mycteroperca olfax* as predominantly solitary, although they frequently occur in association with some labrid herbivores that facilitated these two groupers' preying on benthic fishes and crustaceans (Montgomery, 1975; Erisman *et al.*, 2009). None of the two groupers have ever been recorded with other individuals of the same species, presumably due to competition for food (Filkovsky and Hoback, 2011). In contrast, at Malpelo Island several individuals of these two grouper species were involved in hunting during a feeding frenzy, which leads to the presumption that little competition occurs there (even if we have not quantitative data to support the assumption).

Interspecific associations in which great numbers of jacks and sea snakes aggregate in a feeding frenzy have been recorded ("Planet Earth: Shallow Seas"; BBC Natural History Unit, 2006). We suggest that sea snakes may be a functional counterpart of moray eels, as the snakes also are able to explore deep crevices otherwise inaccessible to predatory fishes.

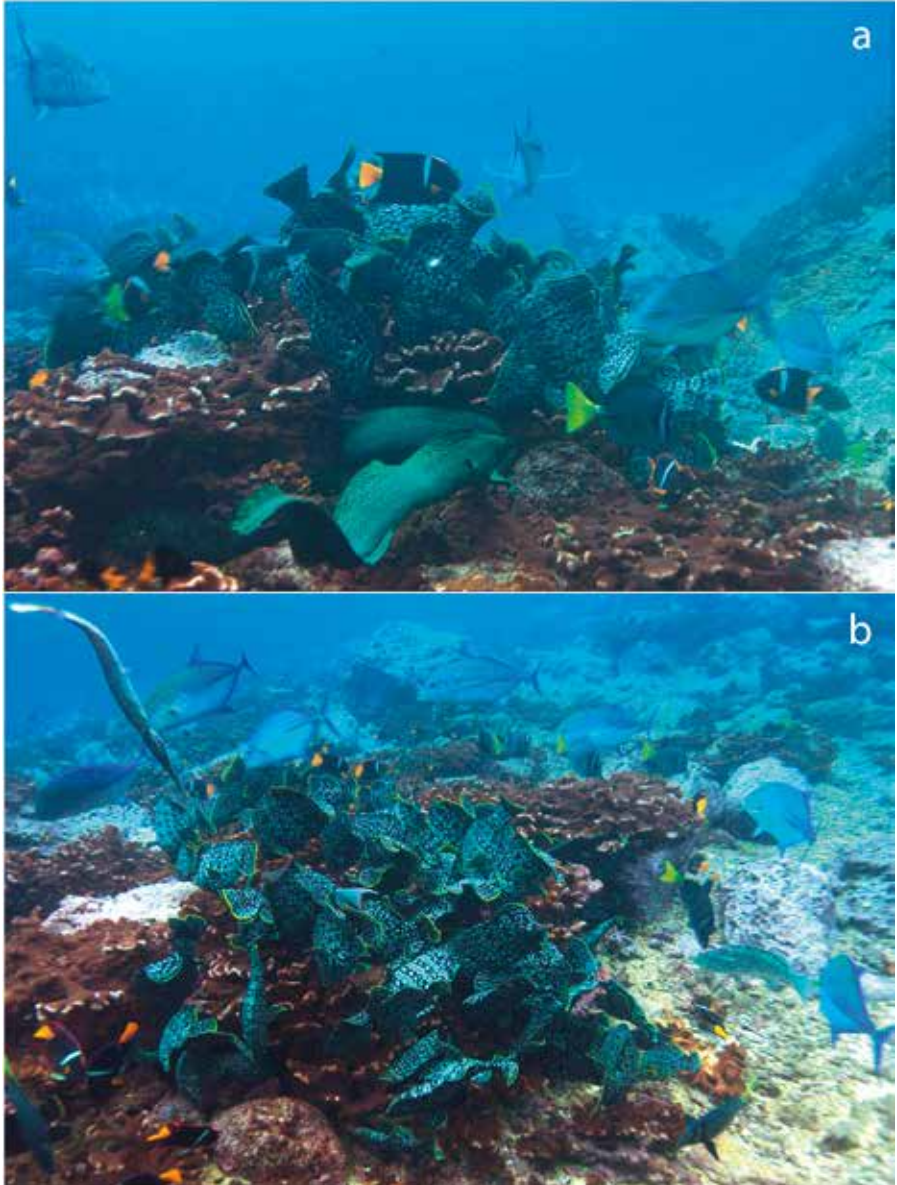


Figure 2. Feeding frenzy within a foraging association at Malpelo Island at 8 m depth, with two *Gymnotherax dovii* individuals in foreground (a) a large aggregation of *Dermatolepis dermatolepis* poking into coral crevices (b), and several *Caranx melampygus* individuals rounding the grouped fishes.



Figure 3. A large aggregation of nuclear-follower species moving close to coral reefs at 10 m depth at Malpelo Island in search of new hunting sites.

Hypotheses about the benefits and costs of the nuclear-follower feeding associations vary. A general view is that the follower species benefit by enhancing prey detection and by gaining easier access to prey types that would otherwise be unavailable (Spotte, 1996; Lukoschek and McCormick, 2000; Sazima *et al.*, 2007). Additionally, fishes involved in the association benefit from increased protection against predators (Roberts, 1996). From these two viewpoints, the nuclear-follower association could be described as an instance of commensalism, since the follower species benefits from the association while the nuclear species is not affected (Aronson and Sanderson, 1987; Lukoschek and McCormick, 2000). However, in some instances the nuclear species may be at a disadvantage due to competition for food, in which case the interaction could be described as a form of “parasitism” (Lukoschek and McCormick, 2000). The hypotheses are not mutually exclusive and, thus, more than one explanation applies to account for the benefits and/or disadvantages of different types of multispecies foraging associations (Krebs, 1973).

At Malpelo Island the great number of follower species (groupers, jacks, hogfish) and their surrounding the reef under inspection by the moray seem to benefit the nuclear species (moray eel) since they do not allow the small fish and invertebrates to flee into the water column. This particular feature may indicate a mutualistic interaction. A similar form of mutualism is reported for a moray eel and a grouper in the Red Sea (Bshary *et al.*, 2006). In this latter case, however, there were fewer participants and the interaction and its duration depended on the hunger level of the groupers. At Malpelo Island, this association does not seem to strongly depend on the hunger level of the associated fishes, since the association was recorded at all times

of the day. The large and multispecies association observed all day long in our study indicates that this type of interaction is very common there and can be an important component of the trophic structure of reef fish assemblages at Malpelo Island.

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