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The Associations between Fishes and Siphonophores

Siphonophores

Siphonophores are polymorphic colonial hydrozoans that inhabit the near shore or offshore water column constituting an important part of the cnidarian's plankton. Like all other hydrozoans, siphonophore nematocysts are restricted to the epidermal layer and their mesoglea is acellular and free of ameboid and other cells. Siphonophore colonies are composed of modified polyps (e.g., feeding gastrozooids and reproductive gonozooids) and medusae (e.g., floating pneumatophores and propelling nectophores) that fulfill different functions and arose through incomplete asexual budding that left them integrated. Functional specialization and integration of these units is so impressive that these delicate and often transparent colonies appear and behave as a single individual. They lack, however, sensory organs such as ocelli found in other pelagic hydrozoans.

The 150 species of the order Siphonophora are split among three suborders: the Cystonectida, Physonectida and Calycophorida. Cystonectids possess pneumatophores but lack water-jet producing nectophores. Physonectids possess both pneumatophores and nectophores. Calycophores possess nectophores but lack pneumatophores. Members of all three suborders feed on zooplankton (Pechenick, 2005; Ruppert *et al.*, 2006). Cystonectids feed mainly on fish larvae while physonectids and calycophores feed mainly on large and small copepods, respectively (Purcell, 1981a). The differences in the type of foods that siphohophores ingest were ascribed to the structure of their nematocysts

(Purcell, 1984a), the size of their gastrozooids (Purcell, 1981a) and their tentacle morphology (Biggs, 1977). The nematocysts of the cystonectids, which either possess threads with no spines or only small spines, are able to penetrate only soft-bodied prey, such as fish larvae, but are not able to penetrate or entangle hard shelled prey, such as crustaceans. On the other hand, the nematocysts of physonectids and calycophores possess heavily spined threads that adhere to crustacean body surfaces and entangle their prey (Purcell, 1984a). During foraging siphonophores engage in special fishing behavior that involves extension of their tentacles, deploying a net covered with nematocyst batteries which is either rapidly moved through the water or may be slowly drifting (Biggs, 1977). As the Portuguese man-of-war (*Physalia physalis*) drifts downwind its long tentacles move continuously up and down, fishing the water through which they pass (Lane, 1960). Fishing tentacles may carry contractible branches called tentilla, covered with batteries of stinging cells, which either resemble larvae or copepods and may serve as visual lures for attracting prey (Purcell, 1980). In deep water, rhythmic flicking of red-glowing bioluminescent tentilla may serve the siphonophore *Erenna* sp. to attract mid-water fishes (Haddock *et al.*, 2005).

Siphonophores freely drifting in the water column are in need of defensive measures to reduce their consumption by fishes, turtles and large planktonic invertebrates, such as hyperiid amphipods. The siphonophore nematocysts are of major importance for reducing predation. The blue-headed wrass *Thalassoma bifasciatum*, a feeding generalist and

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a benthic coral reef fish, avoided fresh pieces of tentacles of *Physalia physalis*. However, after deactivation of the nematocysts by freezing or immersion in distilled water the tentacles were readily consumed (Bullard and Hay, 2002). Juvenile *Tremoctopus violaceus* attach to specially modified suckers on their dorsal arms pieces of *Physalia physalis*, which they employ as an effective weapon (Jones, 1963). Siphonophores may startle or blind interlopers by striking visual displays, such as intense blue light emission (Mackie, 1995). This behavior is often accompanied by rapid escape with the aid of the nectophores (Bone and Trueman, 1982). In response to a disturbance *Chelophyes* sp. can reaches velocities of 30 cm/s. A single nectophore contraction drives the colony 2.5 cm forward and a short swimming burst achieved by synchronous contraction of the nectophores would drive it over a distance of 25 cm.

Siphonophore transparency renders more difficult their detection by predators. In preliminary feeding trials several transparent planktonic organisms were ignored by reef fishes, whereas colored ones were attacked (Bullard and Hay, 2002). Some siphonophores have exploited temporal changes in transparency for defense. The sudden blanching during the day of *Hippopdius hippops*, making the normally invisible creature loom up suddenly from nowhere, was suggested by Mackie (1995) to evoke avoidance reactions in potential predators. Siphonophores (e.g., *Physalia physalis*), which belong to the pleustone (i.e., the interface of air and water), are more concealed from aquatic predators due to the fact that part of the colony (i.e., the pneumatophore) is out of the water (Hamner, 1996). According to Bullard and Hay (2002), food strips of very low caloric values with mean soluble protein of less than $0.3 \, mg \, ml^{-1}$ were avoided by several feeding generalist reef fishes when presented in the field. However, food strips with a caloric value of $3 \, mg \, ml^{-1}$ and higher were accepted. Siphonophores with low caloric values are expected to be less vulnerable to predators, indeed in species with high caloric values (e.g., *Physalia physalis* – $9.5 \, mg \, ml^{-1}$ soluble protein) effective defenses were found.

Physalia physalis – the Portuguese Man-of-War

Physalia physalis the magnificent large blue, purple and pink driven by the wind siphonophore, was aptly named by seaman in the latter part of the fifteenth century – the Portuguese man-of-war – due to its resemblance to a Portuguese caravel (Totton, 1960). *Physalia physalis* occurs in all tropical and subtropical waters around the globe. Siphonophore systematists generally recognize only a single species in the genus *Physalia*. However, a recent molecular phylogenetic study based on specimens collected in New Zealand and Australia revealed substantial amounts of cryptic variation (Pontin and Cruickshank, 2012). Occasionally due to heavy winds *Physalia* may be stranded in large numbers or carried away to colder waters (Wilson, 1947). This siphonophore is by far the largest described species of the order with a pneumatophore attaining a length of up to 30 cm and a width and height of 15 cm, with fishing tentacles that may reach a length of up to 12 meters (Lane, 1960). *Physalia*, like all siphonophores, is a colony composed of up to 1000 modified polyps and medusae that differ in their structure and function. The pneumatophore is a hollow, elongated bag filled with gases secreted from a special gland that keeps it floating on the surface. The concentration of carbon monoxide and several inert gases, such as nitrogen, argon and xenon, is higher in the pneumatophore than in the surrounding air (Lane, 1960).

The shape of the pneumatophore may be altered due to isolated muscle fibers and sheets of muscle cells lining the thin membrane of the float. In the laboratory, Bigelow (1891) produced the erection of a sail-shaped crest by blowing on *Physalia* with bellows. Dipping of the float into the water by bending in order to wet its surface on hot days is also achieved by contraction of muscles lining the float (Totton, 1960). The bottle-like shape and the sail-like crest of the float, which is stabilized by the drag of the underbody, enable *Physalia* to track downwind. The appendages and tentacles are located on a bulge, which may be situated either on the left or right side of the float. Right-handed *Physalia* drift 45º to the left of the downwind whereas left-handed *Physalia* drift 45º right of the downwind (Totton, 1960). Totton (1960) suggested that left or right handedness in a particular individual is established on the first windy day that the larva keeps to the surface. According to Woodcock (1997), right and left-handed forms are found in the same population but sail different mirror image courses, leading to different sea water surfaces. The wind-induced Langmuir vortices result in areas of converging and diverging surface waters. The design of *Physalia* is

such that both left and right-handed forms spend maximum time sailing the diverging surface water, adjacent to the upwelling line of the Langmuir vortex, rich with larval fish, the major prey of *Physalia*, and minimum time in the converging surface water, where buoyant drift material might endanger their sailing motion.

Gastrozooids of *Physalia* are similar to polyps but they lack tentacles; however, small batteries of nematocysts edge their lips. In response to food the gastrozooids twist and open their mouths, which they spread to engulf their prey. Digestive enzymes that break down proteins, carbohydrates and fats are secreted and the partly digested food particles can be seen moving up the gastrozoid stalk (Lane, 1960). Intact and isolated *Physalia* gastrozooids are extremely sensitive to reduced glutathione. When exposed to low concentrations of 10^{-5}–10^{-6} M of this substance they twitched, within five minutes opened their mouth and when contacting a solid object, such as a fish or the glass surface of a petri dish, spread their mouths, increasing in size up to tenfold, from a diameter of 1–2 mm to 20–25 mm. Sometimes stimulated gastrozooids even turned themselves inside out. This strong response to reduced glutathione, also reported for other cnidarians such as the freshwater *Hydra*, is highly adaptive, since this substance is released from wounded and decomposing prey (Lenhoff and Schneiderman, 1959).

Different gonozooids attached to the same colony bear male and female reproductive cells. Dactylozooids contain longitudinal muscle elements, which allow them to shorten the fishing tentacles and reel in trapped prey to bring it into the vicinity of the gastrozooids. The entire length of the tentacles is covered with localized swellings, each consisting of a battery of nematocysts. *Physalia* nematocysts consist of cells of two diameters but of only one basic type. They all consist of threads of the same diameter (i.e., isorhizias) which either bear no barbs or only small ones, effective in penetrating soft tissue. The crude extract of the nematocyst is a potent neurotoxin, 75% as poisonous as the venom of the cobra (Lane, 1960). In the laboratory, fish responded immediately to intramuscular injection of lethal doses of the crude venom by hyperventilating and rapid swimming. After five minutes to several hours, depending on the dose, they became disoriented, sank to the bottom and died after one to three hours. Fish also exhibited chromatophoric responses to venom injection, usually blanching at the site of injection and darkening over the surrounding surfaces (Lane and Dodge, 1958). The nematocyst venom of *Physalia* is toxic and sometimes lethal to humans (Halstead, 1978).

Early analysis of *Physalia* toxin structure revealed a highly labile protein complex including glutamic acid and lysine, denatured by heat and treatment with organic solvents such as ethyl ether (Lane and Dodge, 1958). Physalitoxin is the only toxin that has so far been purified and characterized. It comprises 28% of the venom protein and is a large heterotrimeric glucoprotein (Tamkun and Hessinger, 1981). Physalitoxin causes an influx of calcium ions into several different cell types and lysis by permeabilizing the plasma membrane of target cells (Edwards and Hessinger, 2000). Transmission electron micrographs revealed circular lesions in all membranes with lesion diameter pending on venom concentrations (Edwards *et al.*, 2002).

Early reports of *Physalia physalis* feeding habits summarized by Wilson (1947) included fishes such as herring and flying fishes ranging in size between 4 and 10 cm. A detailed study of *Physalia* feeding behavior was carried out by Purcell (1984b) by removing the prey from gastrozooids of a large number of specimens collected in the Gulf of Mexico and the Sargasso Sea. Only soft-bodied prey, including fish larvae, fish, cephalopods and chaetognaths, were ingested. Larval fishes between 2 and 20 mm in length comprised 70–90% of the prey. *Physalia physalis* was estimated to consume daily about 120 fish larvae with a mean digestion time of about seven hours. According to Purcell (1984b), *Physalia* and other cystonectids, such as *Rhizophysa eysenhardti*, which feeds exclusively on fish larvae (Purcell, 1981b), could probably influence the size of harvested fish stocks in areas of high densities of these siphonophores.

Fishes Associated with Siphonophores other than *Physalia physalis*

Little is known about the partnerships between fishes and siphonophores other than *Physalia physalis* (Purcell and Arai, 2001). Five of the six reported cases (Table 4.1) are based on limited observations carried out in deep water from submersibles. *Leuroglossus stilbius* in association with the large physonectid *Apolemia* sp. (Table 4.1; Robison, 1983) was suggested to gain protection from its host tentacles and to feed on the

Table 4.1 Fishes associated with siphonophores other than *Physalia physalis*.

Fish family and species	Siphonophore suborder and species	Location and Depth	References
Fam. Caristiidae *Caristius* sp.	Cystonectida *Bathyphysa conifera*	Veatch Canyon Atlantic Ocean 168 m	Janssen, 1989
Fam. Caristiidae *Paracaristius* sp.	Physonectida Fam. Apolemiidae	Gulf of Mexico 496 m	Benfield *et al.*, 2009
Fam. Caristiidae	Calycophorida *Praya* sp.	—	Lindsay *et al.*, 2012
Fam. Myctophidae *Stenobrachius leucopsanus* (Eigenmann and Eigenmann, 1890)	Physonectida *Apolemia* sp.	North Pacific Ocean 350–450 m	Robison, 1983
Fam. Bathylagidae *Leuroglossus stilbius* (Gilbert, 1890)	Physonectida *Apolemia* sp.	North Pacific Ocean 350–450 m	Robison, 1983
Juvenile fishes	Physonectida *Forskalia tholoides*	Western North Atlantic (observed by scuba divers)	Biggs, 1976

crustaceans adhered to them. Fish stayed with excised and blown away pieces of the siphonophore and likewise associated fishes did not carry out nocturnal vertical migrations but stayed with their host. Some insight into the association between *Caristius* sp. (Figure 4.1) and the bathypelagic siphonophore *Bathyphysa conifera* was gained by combining direct observations from a submarine with information on stomach content analyses and fish morphology (Janssen, 1989). The gaining of shelter by *Caristius* sp. was evident from the fact that the fish tried to hide behind the sipohonophore when approached by a submarine and left its host only when it was already halfway in the collecting cans. *Caristius* sp. feeds on fish that it probably removed from its host together with other soft-bodied prey, such as chaetognaths and salps and pieces of the host polyps. Janssen (1989) suggested that the truncate body structure and the large fan like pelvic fins (Figure 4.1) seem typical for a fish with high maneuverability but not that of an open water piscivore. Finally, hyperid amphipods of a species often observed by Janssen (1989) attacking siphonophores, found in the fish's stomach, were likely collected from the surrounding water, thus benefiting its host. According to Janssen (1989) the increased use of submarines for observing deep water

Figure 4.1 *Caristius* sp. (Reproduced with permission of J. Janssen and R. Gilmor.)

siphonophores is likely to lead to the discovery of new associations. These efforts should be aimed also outside the north Atlantic and particularly at deep water siphonophores of the Indo-Pacific.

Table 4.2 Fishes associated with the siphonophore *Physalia physalis*.

Fish family and species	Juvenile coloration	Association recorded distribution	Number of associated fish per host	References
Fam. Carangidae *Carangoides bartholomaei* (Cuvier, 1833)	About 5 vertical bars on body[2]	Florida current Atlantic Ocean[1]	0.003[1]	Mayo, 1968[1] FishBase[2]
Fam. Carangidae *Naucrates ductor* (Linnaeus, 1758)	Body dark to pale bluish with 6–7 broad dark bands[2]	Florida current Atlantic Ocean[1] China sea[3]	?	Jenkins, 1983[1] FishBase[2] Collingwood, 1868[3]
Fam. Carangidae *Seriola rivoliana* (Valenciennes, 1833)	Olive to bluish green above; lighter below[2]	Florida current Atlantic Ocean[1]	0.0015[1]	Mayo, 1968[1] FishBase[2]
Fam. Carangidae *Seriola zonata* (Mitchill, 1815)	5 dark bands on a silver colored body	Florida current Atlantic Ocean[1]	0.12	Mayo, 1968[1]
Fam. Carangidae *Trachurus lathami* (Nichols, 1920)	Body dark blue dorsally; silver-white ventrally[2]	Florida current Atlantic Ocean[1]	0.11[1]	Mayo, 1968[1] FishBase[2]
Fam. Centrolophidae *Macrorhamphosus scolopax* (Linnaeus, 1758)	Reddish pink; silver below[2]	Florida Atlantic Ocean[1]	?	Jenkins, 1983[1] FishBase[2]
Fam. Coryphaenidae *Coryphaena hippurus* (Linnaeus, 1758)	Pronounced vertical bars on the sides of the body[2]	Florida current Atlantic Ocean[1]	0.003[1]	Mayo, 1968[1] FishBase[2]
Fam. Nomeidae *Nomeus gronovii* (Gmelin, 1789)	Whitish or silvery with dark blue mottling; pelvic fins black[2]	Florida current Atlantic Ocean[1] Indian & Pacific Oceans[3]	1.03[1]	Mayo, 1968[1] FishBase[2] Mansueti, 1963[3]
Fam. Stromateidae *Mupus maculatus* (Gunther, 1860)	Vertical bands or dark blotches; pelvic fins black[2]	Madeira Atlantic Ocean[1]	0.033[1]	Maul, 1964[1] FishBase[2]
Fam. Stromateidae *Peprilus* sp.	—	Florida current Atlantic Ocean	0.0015	Mayo, 1968
Fam. Stromateidae *Peprilus paru* (Linnaeus, 1758)	Pale blue to green above; silvery with a yellow tinge below[3]	Atlantic Ocean[1]	?	Bean, 1903[1] FishBase[2]
Fam. Stromateidae *Peprilus triacanthus* (Peck, 1804)	Body pale blue above; silvery below[2]	?	?	Klingel, 1940[1] FishBase[2]
Fam. Stromateidae *Schedophilus ovalis* (Cuvier, 1833)	Silvery grey	Madeira Atlantic Ocean	0.17	Maul, 1964

Fishes Associated with *Physalia physalis*

A total of 13 species of fishes, most of them belonging to the families Carangidae and Stromateoidae, have been reported in association with *Physalia physalis* (Table 4.2). Except for *Nomeus gronovii* all these species associate with *Physalia* only temporary as juveniles. About half of them possess a juvenile pattern of dark vertical bands (Table 4.2), which is typical for pelagic fishes that associate with cnidarians and floating objects. Except for *Nomeus gronovii* these partnerships occur at relatively low to very low frequencies (Table 4.2). For at least one species, *Mupus maculatus*, movement between hosts has been reported (Totton, 1960). A positive size correlation between *Naucrates ductor* and *Physalia* was reported by Collingwood (1868). This size matching may be due to competition among the fish for larger hosts or to a size-related host preference. All associated species except *Nomeus gronovii* occupy only the area in the vicinity of the siphonopohore float and avoid the long fishing dactylozooids, whereas *Nomeus* occupies both areas (Mayo, 1968; Jenkins, 1983). According to Mayo (1968) all associated fishes except for *Nomeus*, which he trapped with a dip net, died following capture. One of these species *Trachurus lathomi* has often been recovered dead engulfed by the gastrozooids of *Physalia*. A different result was reported by Maul (1964) for *Mupus maculates* and *Schedophilus ovalis* trapped in the same net with *Physalia*. Two hours after capture these fishes developed ragged fins, had bits of membranes missing and their bodies were covered with large weals, all ascribed to being stung by *Physalia*. Ten days later, the fishes completely recovered with their fin membranes grown back.

The association between *Nomeus gronovii* and *Physalia physalis* is facultative and nonspecific for both the fish and the siphonophore. *Physalia* is usually without accompanying fishes; however, more than ten species were reported to associate with this siphonophore (Table 4.2). *Nomeus gronovii* is usually in the company of the Portuguese man-of-war, after which this fish was popularly named the man-of-war fish. However, this fish was also observed free living in a tide pool (Eigenmann, 1894) under a drifting raft south of Hawaii (Gooding and Magnuson, 1967) and in deep water (Haedrich, 1967) or associated with other species of cnidarians such as *Stomolophus meleagris* (Smith, 1907) and *Porpita* sp. (Besdenov, 1960).

The association between *Nomeus gronovii* and *Physalia physalis* is considered the most intimate and enduring among all fish–pelagic cnidarian partnerships (Mansueti, 1963; Horn, 1976). Knowledge about this partnership is limited, despite the fact that this association was described in the nineteenth century (Van Benden, 1876) and is presented as a classic example of symbiosis in many text books. The genus *Nomeus* consists of a single species with an extremely wide distribution (Table 4.2). Surprisingly little is known about the population dynamics, natural history and levels of host occupation by the fish. Zahl (1952) stated that at Bimini most associated fish were 2–3 inch long but giants of eight inches were also encountered. Mayo (1968) presented the only size distribution histograms of associated fish which he collected during February and March in the Florida current in the vicinity of Miami. He was unable to explain the change in the population structure, namely the fish being smaller and more uniform in size in March than in February (i.e., ranging in size between 10 and 35 mm versus 10 and 125 mm, respectively). Frequency of host occupation in the Florida current was high. Some *Physalia* harbored only one fish, others two and three but up to 15 fish were found occupying a single siphonophore. The number of associated fish per host was very high (i.e., about one fish per *Physalia*) compared with that of other associated fishes (Table 4.2).

The mechanism allowing *Nomeus gronovii* to live unharmed with *Physalia* while other fishes are killed by this siphonophore is still debated and unresolved. Zahl (1952) reported that any *Nomeus* that he would net together with *Physalia* and dump in the same bucket would die, whereas fish that were netted by themselves were not stung by *Physalia*. Death of the fish was ascribed by him to the stings by *Physalia*. On the other hand, Mayo (1968) reported that although he netted more than 700 *Nomeus* together with *Physalia* during the course of his study, no death could have been attributed to contact with *Physalia*. Differences in the results of these two reports may be due to the fact that Zahl (1952) kept the fish and siphonophore in the same bucket whereas Mayo (1968) kept them separately. Even without being forced to form contacts, *Nomeus gronovii* occasionally suffers lethal stings from its host both in the field (Garman, 1896; Whitely, 1947) and the laboratory (Jenkins, 1983). Zahl (1952) suggested that *Nomeus* avoided being stung by *Physalia* thanks to its ability to avoid

contact with its host poisonous fishing tentacles: "*Nomeus* has a reliable, almost miraculous technique avoiding any direct contact with the poisonous curtain which surrounds its bower. It's as if a man should live its life in a maze of high tension wires whose touch would mean quick death".

In a laboratory experiment in a large tank, *Nomeus* maintained a safe distance from the fishing tentacles, even when *Physalia* was manipulated to display sharp changes in direction and speed of movement (Jenkins, 1983). The suggestions that *Nomeus* is protected from *Physalia* through its mucus (Rees, 1961; Arai, 1988) or skin structure (Whitely, 1947; Purcell and Arai, 2001) were refuted by Mayo (1968). The level of tentacle adherence to the surfaces of *Nomeus gronovii* and a control fish *Seriola zonata* were similar, suggesting roughly equal degrees of nematocyst discharge. More precisely, histological examination of the percentage of discharged nematocysts on pieces of skin were similar in *Nomeus gronovii* and *Seriola zonata* (i.e., 79 and 88%, respectively). In a laboratory experiment, *Nomeus gronovii* showed considerable resistance to the injection of crude *Physalia* nematocyst extracts. These fish could survive doses as much as 10 times that which would kill other fishes of similar size and type (Lane, 1960). Lane (1960) suggested that *Nomeus gronovii* resistance may be due to either the development of antibodies to the siphonophore toxins or an innate toxin neutralizing mechanism. This issue is still not resolved more than fifty years later. Tests for presence of antibodies in *Nomeus gronovii* serum to crude extracts of *Physalia* nematocysts were inconclusive. There was a weak antibody–antigen response, mainly ascribed to the thermolability of the toxins and their rapid enzymatic autolysis. Moreover, the monitored reaction may have been between the antibody and a nontoxic component of the extract, thus not necessarily implying inactivation of the toxin (Mayo, 1968).

Two mechanisms seem to protect *Nomeus gronovii* from *Physalia physalis*: avoidance of contact through extreme maneuverability and high levels of resistance to the siphonophore toxins. *Nomeus gronovii* differs considerably from the Indo-Pacific anemone fishes of the genera *Amphiprion* and *Premnas*, which are associated with giant sea anemones. An acclimation process common among anemone fishes removed for several days from their host was never observed in *Nomeus gronovii*. Acclimated anemone fishes are never stung by their hosts and when threatened dive into the sea anemone forming strong physical contacts. In contrast, threatened *Nomeus gronovii* seek the proximity of *Physalia* but avoid contact.

Nomeus gronovii is a stromateoid fish, a member of a small group of medium-sized pelagic fishes that are characterized by toothed saccular outgrowths in the gullet. Most are associated with pelagic cnidarians and floating objects when young but are poorly known as adults (Ahlstrom *et al.*, 1976; Haedrich, 1967). The larvae and juveniles of stromateoid fishes which occupy the surface layers possess a relative small euphysoclistous swim bladder. This swim bladder regresses in all members of this group, except *Nomeus gronovii*, with their transition from juvenile to adult stage and the shift to deeper waters. Only *Nomeus gronovii*, which continues to occupy the upper layers of the water together with its host, retains its functional swim bladder (Horn, 1976). Young of most stromateoid fishes have a banded or blotched pattern, which according to Haedrich (1967) serves as a protective coloration beneath the shifting shadows of objects such as jellyfishes. The adults of these fishes, which occupy deeper water, are usually uniform in color or dark above and pale below. *Nomeus gronovii*, which maintains its association with *Physalia physalis* longer than any other stromateoid, also retains its mottled color pattern, even in the largest examined specimens. Two physical traits of *Nomeus gronovii* that contribute to its exceptional maneuverability are its relatively large number of vertebrae (Purcell and Arai, 2001) and its large pelvic fins, which can be spread like a fan (Jenkins, 1983).

Physalia physalis provides *Nomeus gronovii* with both shelter and food. In the field, fish threatened by an approaching boat or net moved very close to the siphonophore (Mayo, 1968). In the laboratory in large tanks, *Nomeus* would circle a newly introduced host both in a clockwise and counterclockwise direction, remaining 10–20 cm from the main body of the tentacles (Jenkins, 1983). The actual protection of *Nomeus* from piscivore fishes thanks to its association with *Physalia* has not been tested. Stomach content analyses based on specimens of *Nomeus gronovii* larger than 30 mm collected in the field revealed that these fish ingested mainly their host. In their intestines 93% of the nematocysts were undigested and excreted by the fish in fecal pellets containing packed, intact nematocysts (Mayo, 1968). In the laboratory fish larger than 30 mm

attacked their host, ingesting both gastrozooids and small dactylozooids but avoided large dactylozooids (Kato, 1933; Mayo, 1968; Jenkins, 1983). According to Mayo (1968), stomachs of *Nomeus gronovii* smaller than 30 mm that were collected in the field contained mainly planktonic copepods and fish eggs but lacked *Physalia* tentacles or nematocysts. In the laboratory, fish within this size range refused to ingest *Artemia,* or chopped pieces of *Physalia, Porpita* sp. and fish. The difference in the feeding behavior of small and large fish may be due to the size-related ability of fish to endure stinging by *Physalia* while feeding on it. The smaller, more sensitive fish may have to cross a minimal size threshold before shifting to feeding on *Physalia.* Alternatively, the minute dimensions of the mouth and dentition of the smaller fish may render them ineffective in feeding on *Physalia.* The cost to the fish from being associated could be extremely high, since stings from *Physalia,* which are usually mild, could also be lethal. However, it is not known how frequently this may happen in the field and whether the fish consumed by *Physalia* were sick or weak individuals.

An additional cost to the fish from being associated with a drifting siphonophore may be its movement into unsuitable areas. *Physalia physalis* was suggested to benefit from its association, with *Nomeus gronovii* acting as a lure attracting prey to the siphonophore (Tooton, 1960). However, no support for this suggestion has been presented. Moreover, it is currently known that the prey of *Physalia* consists mainly of small larval fishes (Purcell, 1984b) that are not attracted to *Nomeus gronovii.* Finally, in the laboratory *Physalia* may be killed by a large school of *Nomeus gronovii* which consume it. In the field, *Physalia* appears to have a full complement of tentacles regardless of the number of fish present. Probably the rate of feeding on the tentacles by the fish is counterbalanced by *Physalia* growth and budding (Mayo, 1968).

Among the unresolved issues related to the partnership between *Nomeus gronovii* and *Physalia physalis* are the lack of knowledge concerning the sensory modalities and cues involved in host localization and selection. No sexually mature *N. gronovii* have been found (Haedrich, 1967) and, therefore, nothing is known about the reproductive behavior of these fish and the fate of sexually mature individuals. There are considerable difficulties in carrying out research on this partnership, which may be the reason for the lack of knowledge. So far, researchers have been unable to maintain *Physalia physalis* and *Nomeus gronovii* smaller than 30 mm in captivity. Very large tanks are needed to study pelagic organisms in captivity in order to avoid artifacts, such as described by Mayo (1968), of *Nomeus* bumping into the glass panels of small aquaria. The study of this partnership in the field is particularly difficult because it requires open sea diving and the diver has no objects to hide behind, thus affecting the behavior of *Nomeus.* Fish remain closer to their host when observed in the sea by a diver than when observed from land from an overhanging rock (Mayo, 1968).

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