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New Host and Geographical Distribution for the Pearlfish *Carapus mourlani* (Carapidae) with a Discussion on its Biology

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Specimens of the pearlfish *Carapus mourlani* (Carapidae) were observed for the first time in association with the sea cucumber *Isostichopus fuscus* (Holothuroidea: Echinodermata) along the coast of Ecuador. Out of 4345 sea cucumbers collected from various depths between 5 and 60 m, 12 harbored a pearlfish either in the coelomic cavity, the respiratory tree, or the digestive tract, yielding a prevalence of ca. 0.0028. The presence of *C. mourlani* appeared to be detrimental to the holothurian host in some cases. Side effects resulting from coelomic cavity infections included less advanced gonad maturity (reduced gonadal tubule diameter and length, lower ratio of mature oocytes) and a significant proportion of necrotic and shriveled gonadal tubules, devoid of gametes. Aside from discussing this evidence, the present paper briefly describes the biology of the pearlfish, its relationship with the host, and its daily activity cycle.

THE Carapini tribe comprises a group of marine fishes that are distributed worldwide between 40°N and 30°S but display a greater diversity in tropical latitudes (Williams, 1984; Markle and Olney, 1990; Nielsen et al., 1999). The Carapini are currently divided into two genera: *Carapus* and *Encheliophis* (Markle and Olney, 1990; Parmentier et al., 2000a). Among the seven known commensal species of *Carapus*, four are associated with holothurians (*C. acus*, *C. bermudensis*, *C. boraborensis*, and *C. homei*), one is found in sea stars (*C. mourlani*), one is hosted by bivalves (*C. dubius*), and the last one (*C. sluiteri*) by ascidians (Markle and Olney, 1990; Parmentier et al., 2000a; Eeckhaut et al., 2004). The five species that belong to the genus *Encheliophis* are parasites of holothurians (Parmentier et al., 2000a; Parmentier and Das, 2004) although at least two (*E. gracilis* and *E. sagamianus*) were also found in sea stars (Arnold, 1956; Cheney, 1973; Markle and Olney, 1990). Carapidae are known to associate with preferred hosts (Trott and Trott, 1972; Gustato et al., 1979), but they may occur in uncharacteristic hosts as well (Smith, 1964; Trott, 1970). In captivity, some Carapidae were observed to associate with holothurians in which they had never been found before in the wild, although they always selected their customary hosts when given a choice (Trott, 1970, 1981).

While the biology of some Carapidae has received a certain degree of attention, the habits and behavior of *C. mourlani* remain poorly known. *Carapus mourlani* is commonly found in the Indo-Pacific where it is described as a commensal of sea stars such as *Culcita* sp. and *Acanthaster planci* (Meyer-Rochow, 1977, 1979; Trott, 1981). *Carapus mourlani* has been observed to swim along the ambulacral groove of the sea star *Culcita* before entering the stomach, tail first, through the oral cavity and finally reaching the coelomic cavity (E. Parmentier, pers. obs.). The presence of a pearlfish is usually not believed to be detrimental for hosts (Trott, 1981; Vanden-Spiegel et al., 2000), which display very efficient regeneration capabilities (Mary Bai, 1971; Hamel and Mercier, 2000).

The prevalence of pearlfishes in given hosts seems largely dependent on the host abundance and distribution as well as on the occurrence of pearlfish planktonic eggs and vexillifer larva (Trott, 1981). The degree of infection varies between 10% and 100% depending on the species and geographical locations (Jangoux, 1987, 1990).

This paper reports the first occurrence of a Carapini off the coast of Ecuador within a new holothurian host. The specific goals of the present study were to identify the species found in Ecuador and describe the main aspects of its biology.

MATERIALS AND METHODS

Collection and observations.—Sea cucumbers (*Isostichopus fuscus*) were routinely collected by SCUBA divers between 5 and 60 m at several sites along the coast of mainland Ecuador, from fall 2000 to fall 2003, for the purpose of aquaculture studies. During this time, a total of 12 pearlfishes were found inside the sea cucumbers, mostly in fall 2001 and exclusively in hosts collected at 20 ± 5 m near the villages of Punta Ayangue (01°59′33″S and 80°45′23″W) and Anconcito (02°19′60″S and 80°52′60″W) in the Guayas Province. The pearlfishes were either

observed at the time of collection or during the first night of their arrival at the laboratory. While only one specimen, found on 12 September 2003 in Punta Ayangue, was preserved for taxonomical analysis (SIO 04-163, 67 mm SL), all pearlfishes found were of the same species, based on thorough visual inspection and known occurrences of Carapini in the region. The sea cucumbers, collected from two sites off the village of Playas and one site near the city of Machala, did not harbor any pearlfish.

Observations on the behavior of the sea cucumber and the pearlfishes were carried in nine round 20-ton tanks (ca. 4 m wide and 1.5 m high, filled with ca. 35 cm of water). Adult sea cucumbers (18–23 cm long, contracted length) were distributed evenly with an average of 133 individuals per tank and fed daily by adding grinded macrophytes and sedimented phytoplankton. They were provided with a flow of ca. 7000 L/h with natural variations of salinity, pH, and temperature. The light intensity and photoperiod also fluctuated with the ambient conditions (through a Plexiglas™ roof); sunset was around 1845 h. The bottom of the tanks was covered with ca. 30 cm of natural sand collected from the field and a few fiberglass plates to provide shelter to the sea cucumbers. Sea cucumbers harboring a pearlfish were randomly spread among the tanks; no more than 3–4 infected individuals were ever observed in a given month. Monitoring began on the first day of collection, from 30–45 min before sunset through the early morning hours and for up to 14 consecutive nights, depending on the level of activity noted. Observers used low intensity light sources to confirm a specific observation when necessary, otherwise using only natural lighting.

In the experiments designed to determine the importance of light in the behavior of *C. mourlani*, the tanks containing infected sea cucumbers were either exposed to artificial fluorescent lights (ca. 100 μmol m^{-2} s^{-1} in the first five cm of water) or covered with opaque plastic. Every simulation was repeated at least three times in the night and day time and the results compared to observations under the normal day/night regime. After the general observations were completed, the pearlfishes were routinely separated from their host and transferred to a 40 L aquarium offering environmental conditions similar to the ones prevailing in the larger tanks, to verify if the fishes could survive away from their hosts.

All sea cucumbers that initially harbored a pearlfish and those that were visited by one during the experiments were identified and eventually dissected. They were examined for signs of morphological and tissue alteration. Special attention was given to the two females in which *C. mourlani* was present in the coelomic cavity, as they displayed evident abnormalities. Qualitative and quantitative measurements were therefore taken in fresh gonad samples collected from infected (n = 2) and non-infected female sea cucumbers (n = 30). The dominant gametogenic stage of maturity was determined using the classification of Hamel et al. (1993, 2001). The following features were observed: 1) the proportion of gonadal tubules displaying necrotic sections (e.g., dehydrated and shriveled, darker in color, irregular in shape and in diameter); 2) the length, outer diameter, and lumen diameter of 15 randomly collected gonadal tubules (in infected individuals, data were collected separately in necrotic and normal sections); 3) the diameter and maturity level of 30 oocytes; 4) the number of mature oocytes per cm in three gonadal tubules.

Taxonomic investigation.—Counts and measurements followed the methods of Williams and Shipp (1982) and Markle and Olney (1990). A Wild M10 binocular microscope, combined to a camera lucida, was used. Measurements were made to the nearest 0.1 mm with a caliper. The specimen from Ecuador available for the description was stained with alizarin (Taylor and Van Dyke, 1985) and compared to other stained specimens of the Carapini (*Carapus boraborensis*, *C. homei*, *C. dubius*, *C. mourlani*, *C. acus*, *Encheliophis gracilis*, and *E. vermicularis*) from the private collection of the laboratory of Functional and Evolutive Morphology of the University of Liège, Belgium.

Results

Description.—The following description is restricted to the characters that allowed the identification of the Ecuadorian specimen. Outer cardiform teeth are present at the anterior end of the premaxilla, and small conical teeth are organized in two rows along this bone. The dentary displays a row of large external conical teeth and three to five rows of smaller conical teeth. The vomer has three large prominent teeth. The first ceratobranchial displays three well-developed branchiospines, with two rows of small conical teeth. The specimen also has a central constriction of the swim bladder at the 9th vertebra, 15 precaudal vertebrae, and 19 rays in the pectoral fin.

Biological aspects.—A total of 12 pearlfishes were found individually in separate hosts: five in Punta Ayangue samples and seven in Anconcito sam-

ples, out of 4345 sea cucumbers collected at those sites over a period of three years. Two gravid females were observed, and no juvenile was ever found, giving a male to female ratio of 2 : 10. Although they were kept for variable lengths of time, all sea cucumbers were eventually dissected. The prevalence of *I. fuscus* infected by *C. mourlani* in the Punta Ayangue-Anconcito region was therefore 12 : 4345, or ca. 0.0028. However, pearlfishes were never observed in thousands of other sea cucumbers collected at three other sites during the same period.

Monitoring of the behavior of *C. mourlani* in captivity showed that they remained inside their host during the day. They first started to come out around 1930 h (ca. 45 min after sunset), although they usually only exposed half of their body in a back and forth motion. As darkness settled (ca. 2000 h), the pearlfishes left their hosts and swam freely for periods varying from 30 to 95 min before sheltering again for period of 32 to 55 min and heading out once more. The cycle was usually repeated several times each night (between two to four times, depending of the individual). The same individual was often found to swim out of its host several nights in a row, for up to 12 consecutive nights in one case. Some fishes remained active until 0100 h with a peak of activity noted just after emergence from the host. A tendency to swim actively, explore shelters and crevices, and probe the anal opening of several sea cucumbers was observed. In fact, the same fish rarely came back to its original host after foraging. *Carapus mourlani* were found to graze on various substrates comprising the fouling layers of the tanks and fiberglass plates, mainly on a mixture of hydrozoans, worms, crustaceans, and various other sessile benthic invertebrates as well as on the surface of sea cucumbers. Artificial light (ca. 100 $\mu mol\ m^{-2}\ s^{-1}$) prevented the pearlfishes from swimming out of the hosts at sunset. When light was switched off again, it generally took under 10 min for most pearlfishes to exit the holothurians. Conversely, when darkness was simulated during daytime, the foraging behavior of *C. mourlani* was induced within a period of ca. 45 min. Pearlfishes did not survive more than ca. six days in the absence of their host, at least in the conditions provided during the study.

Inspection of the originally infected sea cucumbers revealed that four of the specimens of *C. mourlani* lived in the last third of the digestive tract, six of them colonized the respiratory tree, and two dwelled in the coelomic cavity of *I. fuscus*. Hosts harboring a pearlfish in the intestine or respiratory tree did not present any deformity or internal injury. However, the two cases of coelomic cavity infection were characterized by the presence of multiple openings along the respiratory tree epithelium. Necrotic or shriveled tissues were observed along the respiratory tree and gonad, and evidence of irritation of the body wall muscles bands and of the cloaca were visible. Furthermore, the gonad development of these two female hosts was clearly less advanced than that of non-infected sea cucumbers collected simultaneously (Table 1). The infections of *C. mourlani* were noticed in *I. fuscus* that had been collected between two and five days before the monthly spawning date depending on the month. During that period, >90% of the sea cucumbers were ready to spawn and displayed gonadal tubules filled with mature gametes. However, individuals hosting a pearlfish in the coelomic cavity were predominantly in the ''growth stage,'' which is characterized by less abundant and less developed gametes with poor vitelline reserves. Moreover, the proportion of necrotic tubule sections, which were devoid of gametes, was clearly higher (ca. 34%) in infected sea cucumbers than in non-infected ones (ca. 4%). Finally, the gonadal tubules of infected individuals were shorter and smaller; they had less gametes per centimeter and a strikingly thinner lumen (Table 1).

Discussion

Identification of SIO 04-163.—*Carapus* lacks pelvic fins and fangs and diastemas on the premaxilla and dentary. The premaxilla bears cardiform teeth, two or three enlarged teeth on its anterior part, and at least two rows of small conical teeth along its length, whereas the dentary has one row of enlarged conical teeth and several rows of small internal teeth (Parmentier et al., 2000a). Therefore, the SIO 04-163 specimen definitely belongs to the genus of *Carapus*. It can further be classified as *C. mourlani* on the basis of the combination of the following characters: swim bladder constriction at the ninth vertebra, three prominent teeth on the vomer, 15 precaudal vertebrae, 19 rays in the pectoral fin, and two rows of teeth on the branchiospines of the first ceratobranchial (Petit, 1934; Markle and Olney, 1990; Parmentier et al., 2002a).

Biological aspects.—Frequency of infection of holothurians by Carapidae vary between localities. Out of 257 specimens of *Bohadschia argus* collected in French Polynesia, 84% contained pearlfishes: *C. homei* in 39.3% of the cases and *C. boraborensis* in 59.2% (Parmentier and Vandewalle, 2005). VandenSpiegel and Jangoux (1989) reported similar data. Tyler et al. (1992) and

TABLE 1. GONAD MATURITY AND MORPHOMETRIC MEASUREMENTS OF *Isostichopus fuscus*. Comparison between non-infected individuals ($n = 30$) and infected individuals hosting a pearlfish in the coelomic cavity ($n = 2$). Values are expressed as mean ± confidence interval (95%).

	Non-infected		Infected			
			Normal tubules		Necrotic tubules	
	Mature		Growth		No gametes present	
Dominant gametogenic stage	Mean ± CI	*n*	Mean ± CI	*n*	Mean ± CI	*n*
Gonadal tubule length (mm)	95.6 ± 0.8	450	82.3 ± 1.6	30	61.1 ± 7.6	30
Gonadal tubule diameter (mm)	3.7 ± 0.5	450	2.8 ± 0.3	30	2.1 ± 0.2	30
Lumen diameter (mm)	1.9 ± 0.2	450	1.1 ± 0.3	30	0.1 ± 0.08	30
Oocyte diameter (μm)	110.7 ± 3.1	900	55.2 ± 7.5	60	–	–
No. of oocytes per cm of gonadal tubule	334.4 ±18.9	90	202.7 ± 31.4	6	–	–

Smith et al. (1981) noted a frequency of infection of 21% by *C. bermudensis* in Bahamas and of 8 to 13% by *C. acus* in the Mediterranean Sea (Kloss and Pfeiffer, 2000). However, the occurrences of *C. acus* apply only to hosts sampled at ca. 40 m; no pearlfish was ever found in holothurians collected from shallower depths in Corsica (E. Parmentier, pers. obs.). The prevalence found in the present study (ca. 0.0028) is probably the lowest ever recorded. The fact that Carapidae appear to be restricted to certain depths, as observed in the Mediterranean and in the present study, may partly account for this very low incidence since the 4345 sea cucumbers were collected between ca. 5 and 60 m throughout the study. However, this value does not take into account the thousands of other *I. fuscus* collected elsewhere along the Ecuadorian coast, which were never reported to host a pearlfish.

Despite the low frequency of infection, two gravid pearlfish females were found, which raises questions regarding the recruitment and overall reproductive success of the population of *C. mourlani* found in *I. fuscus*. Investigation of other potential Ecuadorian hosts such as sea stars (e.g., *Oreaster occidentalis*, *Heliaster multiradiata*) could shed some light on the situation.

To our knowledge, no study has ever been conducted to evaluate the impact of pearlfishes on their hosts. Adverse effects can be expected in the case of species of *Encheliophis* which feed on the host's gonads (Murdy and Cowan, 1980; Trott, 1981; Parmentier and Das, 2004). However, *C. mourlani* are commensals that feed outside of their hosts (Parmentier and Das, 2004). The present work is the first to suggest possible detrimental effects of a *Carapus* on holothurians. The two hosts in which *C. mourlani* were found inside the coelomic cavity showed evidence of tissue alterations and less advanced gametogenic levels of maturity compared to other infected and non-infected sea cucumbers collected in the same location and to transient hosts visited by pearlfishes during the experiments. Previous studies have shown that the reproductive cycle of populations of *I. fuscus* is generally characterized by a well synchronized gonad development and monthly spawning (Mercier et al., 2004). By tearing the respiratory tree to reach the coelomic cavity, the pearlfish would allow sea water to penetrate as well, therefore modifying the composition of the perivisceral coelomic fluid, which has been identified as a key element in the reproductive cycle of echinoderms (e.g., Hines et al., 1992; Barker and Xu, 1993; Mercier and Hamel, 2002).

Carapidae usually occur in the respiratory tree or coelomic cavity of holothurian hosts (Trott, 1970; VandenSpiegel and Jangoux, 1989; Markle and Olney, 1990). The presence of specimens of *C. mourlani* in the digestive tract remains anecdotal and is considered unusual. In this study, the presence of a pearlfish in the digestive tract was always consistent with the absence of intestinal contents and might therefore represent a laboratory artifact. In the field, *I. fuscus* usually feed continuously during the night, so they should almost always present some sort of intestinal contents, whereas diurnal inactivity reduces intestinal transit and the intestine usually remains at least partly full until the next feeding period (Mercier et al., 1999, 2004). Sheltering of pearlfishes in the respiratory tree remains the most consistent observation and it appears to be the most suited place for the fish to dwell (i.e., allowing gill oxygenation through periodic water exchange).

The activity of *C. mourlani* monitored during this study was clearly nocturnal. This behavior agrees with the notion that the eyes of *C. mourlani* share certain characteristics with those of cave-dwelling organisms, such as photoreceptors with

high levels of sensitivity and poor resolution (Meyer-Rochow and Tiang, 1978). The fact that the pearlfishes were found to leave their host almost every night while in captivity is not necessarily an indication of their normal behavior. Indeed, other evidence suggests that wild pearlfishes may remain in the same host for a while. For instance, less advanced gametogenic levels of maturity and gonadal tissue deterioration were recorded in sea cucumbers that hosted a pearlfish in their coelomic cavity. Since gonad development cannot be altered within one or two days (Hamel and Mercier, 1996, 1999), and the pearlfish-to-host ratio does not seem sufficient to allow repeated infections, the delayed gonad development should be induced by long-term infection. Moreover, based on otolith (sagittae) observations, Parmentier et al. (2002b) proposed that *C. boraborensis* and *C. homei* had resting and active periods, with a duration that depended on the energy provided by the ingested prey. In *C. bermudensis*, a feeding periodicity ranging from 15 to 24 days on average was estimated (Smith et al., 1981). The nightly activity recorded in the tanks could therefore be linked to the abundance of copepods and other invertebrates that live on the outer surface of holothurians. Although stomach contents were not examined during this study, previous data have shown that shrimp, decapods, annelids, and small fish form the usual diet of *C. mourlani* (Meyer-Rochow, 1979; Parmentier and Das, 2004).

The identification of a new holothurian host for *C. mourlani* in Ecuador seems to support the observation that this species can shelter in sea cucumbers that are not hosting other Carapidae (Markle and Olney, 1990). In parts of the world where sympatric *Carapus* species occur, *C. mourlani* is found in sea stars such as *Culcita novaeguineae*, *C. schmidelliana*, *Acanthaster planci*, and *Choriaster granulatus* (Eeckhaut et al., 2004). On the west coast of Central America, *C. dubius* generally shelters in bivalves (Castro-Aguirre et al., 1996; Paredes-Rios and Balart, 1999; Parmentier et al., 2000b), whereas *E. vermicularis* favors sea cucumbers (Markle and Olney, 1990) although they have never been reported in *I. fuscus* so far.

Material Examined

Institutional abbreviations as follows: SIO = Scripps Institution of Oceanography; PCL = Private Collection of the Laboratory of Functional and Evolutive Morphology in Liège (Belgium).

Carapus mourlani. SIO 04-163, 67 mm TL, Ecuadorian coast, Punta Ayangue, 01°59′33″S, 80°45′23″W; PCL, 75 mm TL, French Polynesia, Moorea (1 specimen), 70–110 mm TL, Madagascar, Tulear (3 specimens). *C. boraborensis*. PCL, 130–180 mm TL, French Polynesia, Moorea (3 specimens). *C. homei*. PCL, 80–125 mm TL, French Polynesia, Moorea (2 specimens). *C. dubius*. PCL, 92–120 mm TL, Gulf of California, Bay of la Paz, Esperitu Santo Island (2 specimens). *C. acus*. PCL, 74–125 mm TL, Bay of Calvi, Corsica (4 specimens). *Encheliophis vermicularis*. VIMS 09600, 123–148mm TL, New Caledonia (2 specimens). *E. gracilis*. PCL, 135–196 mm TL, French Polynesia, Moorea (2 specimens).

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