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Association between the squat lobster *Gastroptychus formosus* and cold-water corals in the North Atlantic

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Although there are no previous descriptions of the habits of chirostylids in the North Atlantic, it is likely that species in the genera Uroptychus, Eumunida and Gastroptychus have close ecological ties with deep-sea corals since they have all been recorded in trawl samples containing corals from >200 m depth. We analysed in situ distribution of Gastroptychus formosus and potential hosts using a ROV at a range of north-eastern Atlantic sites and found that this species forms a close association with deep-sea corals that resembles the chirostylid–anthozoan associations reported in shallow Indo-Pacific waters. We update the known distribution for G. formosus, confirming that it is an amphiatlantic species that occurs along the Mid-Atlantic Ridge at least as far south as the Azores and along continental margins from the Canary Islands to Scotland at depths of 600–1700 m. The adults have very specific habitat preferences, being only found on gorgonian and anti-patharian corals with a strong preference for Leiopathes sp. as a host. This highly restricted habitat preference is likely to render chirostylids vulnerable to the impacts of demersal fishing both directly, as by-catch, and indirectly through habitat loss.

Keywords: cold-water corals, deep sea, north-eastern Atlantic, squat lobster, *Gastroptychus*

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INTRODUCTION

Intricate ecological associations between anthozoans and crustaceans (including Amphipoda, Caridea, Majidae, Porcellanidae, Latreillidae and Galatheidae) are well known in shallow, warm-water ecosystems (Goh *et al.*, 1999; Wirtz & d'Udekem-d'Acoz, 2001; Castro *et al.*, 2003; Jonsson *et al.*, 2004). Although such associations are less well known in cold-water habitats, recent research is beginning to reveal that similar interactions may also be common in the deep-sea. In the North Atlantic, for example, Caridea and Galatheidae are common cryptic inhabitants of reefs formed by the scleractinians *Lophelia pertusa* and *Madrepora oculata* (Jensen & Frederiksen, 1992; Mortensen *et al.*, 1995). A newly described amphipod (*Pleusymtes comitari*) is also associated with gorgonian forests at 1 km depth off Ireland (Myers & Hall-Spencer, 2003) and various Crustacea are parasitic on deep-water gorgonians at 330–500 m depth off Nova Scotia (Buhl-Mortensen & Mortensen, 2004).

Our present study describes observations of the chirostylid *Gastroptychus formosus* using a remote operated vehicle (ROV) at numerous sites in the North Atlantic. In shallow waters of the temperate North Pacific chirostylids are known to occur predominantly on gorgonian corals (Osawa & Nishikiori, 1998; Baba, 2005). In the North Atlantic, chirostylids have only been found in deep waters and, due to their

inaccessibility, relatively little is known about their ecology. Previous records of *G. formosus* are scarce, although it has been reported across the Atlantic from Nova Scotia to Ireland and south to the Azores along the Mid-Atlantic Ridge at depths of 800–1700 m (Pohle & Macpherson, 1995).

A recent international surge of interest in deep-water coral habitats (Roberts *et al.*, 2006) has led to a series of surveys of north-eastern Atlantic coral habitats providing an archive of high quality *in situ* film (Olu-Le Roy *et al.*, 2002; Huvenne *et al.*, 2005; Lindberg *et al.*, 2007; Roberts *et al.*, 2008; Wienberg *et al.*, 2008). These surveys are beginning to reveal the ecological complexities of newly discovered coral reef habitats and underpin our advancing knowledge of how to manage deep-sea habitats (Davies *et al.*, 2007). In this study we adopt the approach taken by Costello *et al.* (2005) who used film from a variety of sources to investigate how fish interact with temperate coral reefs. Based on an analysis of film from multiple deep-sea surveys this study aims to establish whether the chirostylid–anthozoan association found in Indo-Pacific waters also occurs in deep-sea areas of the north-eastern Atlantic and if habitat use of *G. formosus* differs among deep coral reefs at regional scale.

MATERIALS AND METHODS

Data on the distribution of *Gastroptychus formosus* (and the synonyms *Ptychogaster formosus* and *Chirostylus formosus*) were compiled from a recent catalogue of squat lobsters (Baba *et al.*, 2008) and original papers from the 'Travailleur' expedition of 1883 (Milne-Edwards & Bouvier, 1900), the

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'Caudan' expedition of 1885 (Caullery, 1896), the 'Prince of Monaco Cruise' of 1901 (Bouvier, 1922), the 'Huxley' in 1906 (Kemp, 1910) were reviewed together with papers by Selbie (1914), Zariquiey Álvarez (1968) and Pohle & Macpherson (1995). In addition, videos from the deep-water North Atlantic cruises 'Caracole', 'Divanaut2', 'Atos' and 'Diapisub' held in the Ifremer photographic library and the 'Ark XIX/3 2003' cruise were examined to note occurrences of *Gastroptychus* sp., as well as photographs from the 'Arqdaço-27-Po7' campaign in the Azores Islands (38.660°N 28.265°W) at 1062–1100 m depth. By-catch specimens and locations were also obtained from fishermen in Le Guilvinec (Brittany, France). Dissections were carried out to sample the stomach contents from two specimens provided by fishermen (carapace lengths including the rostrum were 2.47 and 1.96 cm). Organisms could not be distinguished in the contents using a binocular microscope. Therefore, we examined sub-samples using a scanning electron microscope (SEM).

We studied habitat use and the interactions between *G. formosus* and anthozoans at five sites between 600 and 1200 m depth off Ireland. The sites were Logatchev Mounds (55°32'N 15°14'W) on the edge of Rockall Trough, Pelagia mounds (53°47'N 13°57'W), Giant Mounds (53°06'N 14°55'W) and Twin Mounds (53°06'N 14°54'W) on Porcupine Bank and Thérèse Mound (51°25'N 11°46'W) in the Porcupine Seabight (Figure 1). Visual surveys using ROV 'Victor 6000' were carried out in August 2001 on Logatchev Mounds, Pelagia Mounds and Thérèse Mound

during the 'Caracole' cruise, and in June 2003 on Twin Mounds and Giant Mounds on the 'Ark XIX/3' cruise. One passage of the ROV was completed over each site and resulted in 13 hours of useable video from Thérèse Mound, 23 hours from Giant Mounds, 18 hours from Twin Mounds, 12 hours from Logatchev Mounds and 27 hours from Pelagia Mounds. The ROV position was obtained via an USBL (ultra-short baseline) positioning system with an estimated error of 1% of depth-range. On each cruise the ROV was used to record the biota that occurred on bathymetric highs that had been detected during previous multibeam echosounder surveys (Olu-Le Roy *et al.*, 2002; Klages *et al.*, 2004). Video was recorded on SVHS from two cameras mounted on the ROV; a forward-facing camera was used to aid anthozoan and crustacean identifications and a downward-facing camera for quantitative records of *G. formosus* and host identification. We analysed the distribution of megafauna using only film taken when the ROV was 2–4 m above the sea bed and moving at mean speed of 0.3 m.s⁻¹. Identification of *G. formosus* was not possible when the ROV was >4 m off the seabed or moving >0.5 m.s⁻¹. We were able to identify *G. formosus* based on body shape and the ratio of cheliped to carapace + rostrum length which is more than 4:1 and characteristic of this species of chirostyliid in the north-eastern Atlantic (Hayward & Ryland, 1990). Occurrences of *G. formosus* were recorded only when the limbs were clearly distinguishable to avoid confusion with similar-shaped crustaceans which were observed in

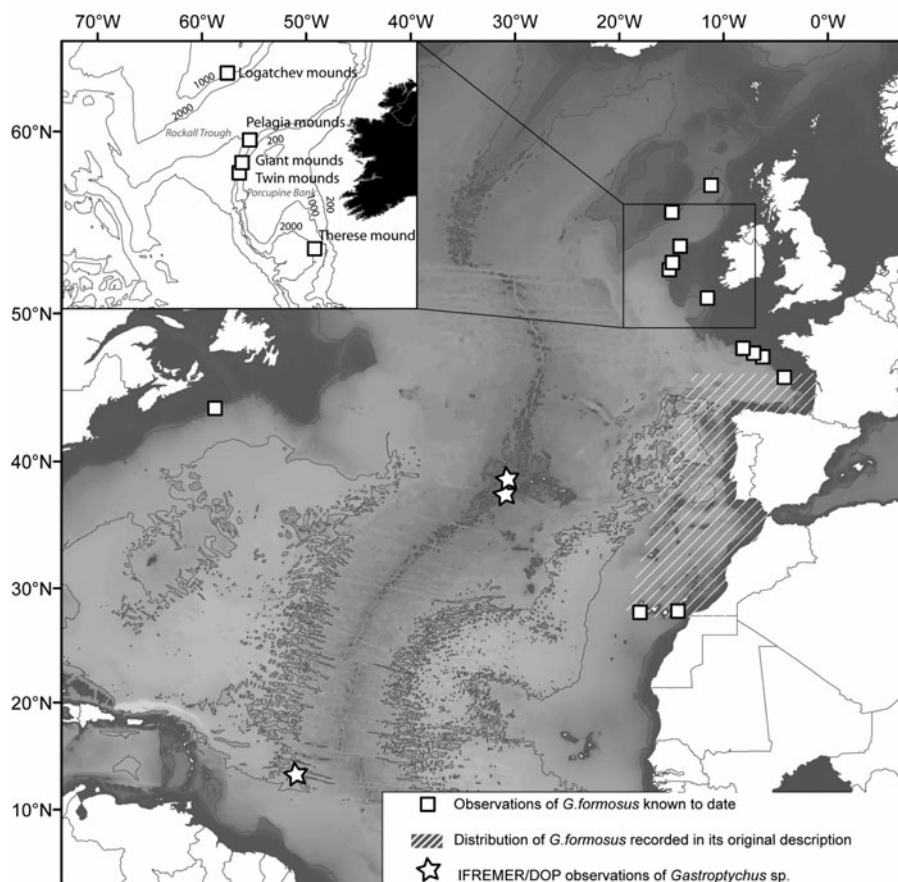


Fig. 1. North Atlantic distribution of *Gastroptychus* sp. and *G. formosus* observations and the distribution of this species according to first description (Milne-Edwards & Bouvier, 1900).

association with anthozoans (e.g. *Rochinia* sp.). Distributions of *Leiopathes* sp. and *Bathypathes* sp. (antipatharians), and *Paramuricea* sp. (gorgonians) were noted along ROV dive tracks based on their shape, size and colouring with reference to voucher material collected with the manipulator arm of the ROV during filming. For each dive we thus obtained records of the abundance of *Leiopathes* sp., *Bathypathes* sp. and *Paramuricea* sp. colonies together with indication of the presence of *G. formosus* on each coral colony observed.

Statistical analysis was carried out with R software using generalized linear models (www.r-project.org). To assess the binomial response variable ($Ngfo_1$ presence of *G. formosus* on coral/ $Ngfo_0$ absence of *G. formosus* on coral) on different hosts and at different sites, the data were analysed using the logistic regression model. This method is widely used in biostatistics to describe the relationship between a response variable, expressed as proportions, and one or more explanatory discrete variables (Hosmer & Lemeshow, 2000; Wasserman, 2004). The Wald-statistic was calculated on all 3 hosts and 5 sites to examine whether these variables were significant predictors in the model. Logistic regression fits the relationship between each variable to an S-shaped curve (logit function) within a range of 0 to 1 (presence/absence of *G. formosus*). The slope estimate shows the positive or negative effect as determined by the parameters.

RESULTS

Compilation of published and unpublished accounts and an analysis of archive video reveals that *G. formosus* occurs on

both the north-eastern and north-western Atlantic coasts and ranges from Darwin Mounds off Scotland in the north to the Azores in the south (Figure 1). Two specimens were provided by local fishermen targeting deep-sea species on the continental margin off Brittany (Figure 2), one of them having a short piece of *Leiopathes* sp. attached to its legs. Still images and image captures of archive video of this association are presented in Figure 3 for various North Atlantic localities. Stomach contents analysis revealed that most of the particles observed using SEM could not be identified except a few pieces of crustacean shorter than 0.1 mm (Figure 4A). It was striking to note that on archive material from Barbados and the Mid-Atlantic Ridge chirostyliids were always found holding onto antipatharians and gorgonians and were never seen on surrounding habitat types or on reef-building scleractinians.

At the five sites where we analysed ROV film quantitatively, *G. formosus* were only found on corals but were never seen on the 1000s of *Lophelia pertusa* and *Madrepora oculata* colonies that form reefs on the tops and flanks of carbonate mounds in this region (Klages *et al.*, 2004). The *G. formosus* were always seen either holding onto the gorgonian *Paramuricea* sp. (which formed dense stands on rock outcrops and among living *Lophelia pertusa*) or were attached to the antipatharians *Bathypathes* sp. and *Leiopathes* sp. The antipatharians were more isolated in occurrence than the gorgonians and were usually attached to boulders and cobbles at the reef periphery or at the base of the mounds. Abundant stands of *Paramuricea* sp. were recorded at Giant Mounds and Thérèse Mound but these hosted only sparse *G. formosus* (Table 1). At four out of five sites the most common chirosty-

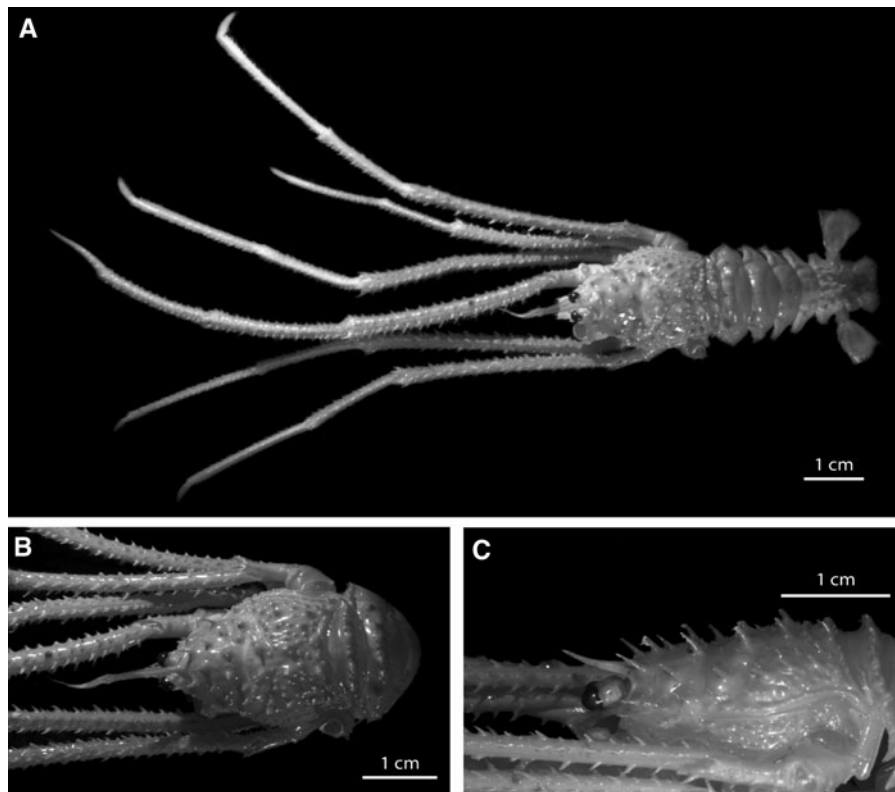


Fig. 2. Anatomical details of *G. formosus* caught in bottom trawls by fishermen on the continental shelf break off Biscay in March 2006 showing (A) characteristically long chela and (B, C) details of the carapace.

lid host coral was *Leiopathes* sp. and *G. formosus* was found most frequently at Thérèse Mound. At this site 261 corals (240 *Leiopathes* sp. and 21 *Paramuricea* sp.) were seen with at least one squat lobster holding onto them (Table 1).

Statistical analyses are summarized in Table 2 where slope estimate and corresponding Wald-test *P* values are given. The results show a significant positive relationship between *G. formosus* presence and the host *Leiopathes* sp. ($P < 0.005$, slope estimate = 1.49) and, with a lesser degree of significance, for the host *Bathypathes* sp. ($P = 0.015$, slope estimate = 0.62). On the contrary, a significant negative relationship between the presence of the squat lobster and *Paramuricea* sp. was found ($P < 0.005$, slope estimate = -2.11). This means that while *G. formosus* is preferentially associated with *Leiopathes* sp., they are not exclusively limited to this host. The *G. formosus* occurred significantly more frequently at Thérèse Mound than the other four sites ($P < 0.005$, slope estimate = 0.63).

Groups of up to nine *G. formosus* were observed on large (1 m tall) *Leiopathes* sp. colonies and these groups included both large and small individuals living together. No aggressive behaviour was noted within the groups during the time of observation, although the approach of the ROV sometimes elicited meral display behaviour, whereby the animals fully extended their chelipeds (Figure 3C). More usually the *G. formosus* exhibited no response to the ROV and were either stationary or seen repeatedly moving their chelae from the coral surfaces to their mouths and back while they collected prey or detritus in their first maxillipeds, possibly indicating that they feed off the coral surfaces.

DISCUSSION

It is likely that species in the genera *Uroptychus*, *Eumunida* and *Gastroptychus* have close ecological ties with deep-sea corals since they have all been recorded in trawl samples containing corals from >200 m depth (Caullery, 1896; Milne-Edwards & Bouvier, 1900; Selbie, 1914; de Saint Laurent & Macpherson, 1990). For instance, association of *Eumunida picta* with various deep water corals have been reported from the north-western Atlantic (Buhl-Mortensen & Mortensen, 2004) and quantitative analysis from video observation of shipwrecks in the Gulf of Mexico showed that *E. picta* occurs primarily in association with *L. pertusa* (Jensen & Frederiksen, 1992; Mortensen *et al.*, 1995; Kilgour & Shirley, 2008). Our analyses of *in situ* observations at a range of north-eastern Atlantic sites show that *G. formosus* forms a close association with antipatharians that is similar to the chirostyliid-anthozoan associations reported in Indo-Pacific waters. *Gastroptychus formosus* has been observed living singly or in groups mainly attached to *Leiopathes* sp. at depths of 600–1200 m. A series of cruises carried out with submersible and ROVs have also recently documented *Gastroptychus* sp. associated with antipatharians on the New England seamounts off the east coast of the USA (France *et al.*, 2006).

Although invertebrate identifications using ROV video film can be difficult, it was relatively easy to identify *G. formosus* by comparing images with by-catch specimens provided by the fishing fleet and specimens held at the Natural History

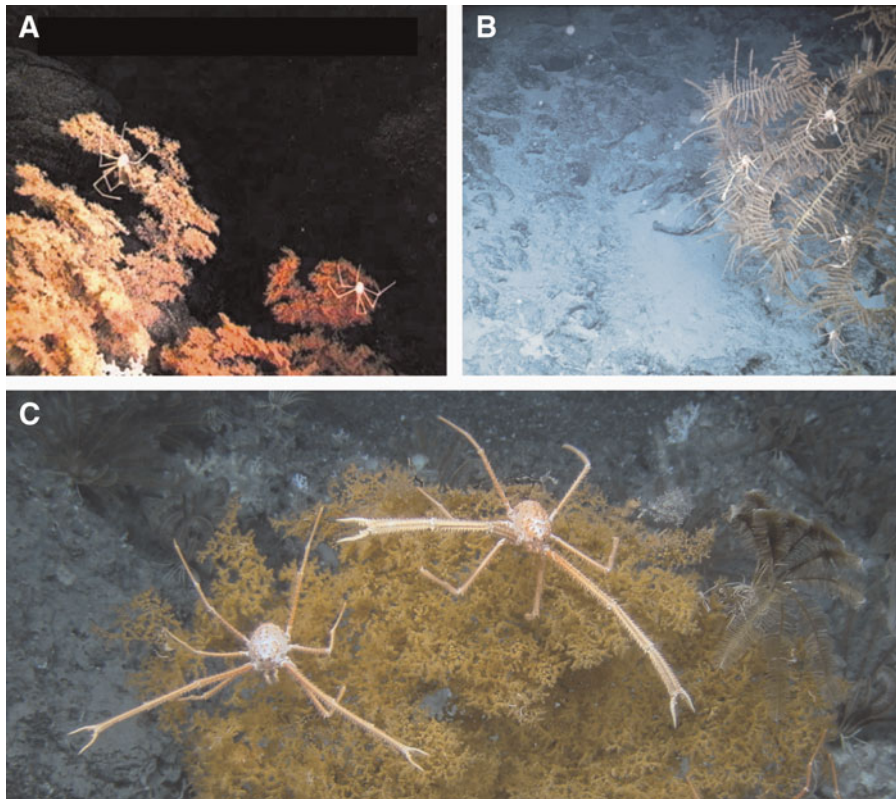


Fig. 3. *In situ* images of *Gastroptychus* cf. *formosus*. (A) Bushy *Leiopathes* sp. at 834 m depth at the Menez Gwen vent site on the Mid-Atlantic Ridge in 1994; (B) likely *Gastroptychus* sp. living on an unidentified antipatharian at 1300 m depth off Barbados in 1992 (11°14'N 59°22'W); (C) meral display of *G. formosus* on *Leiopathes* sp. on the Twin Mounds at 1092 m depth off Ireland in 2003. Images copyright Ifremer.

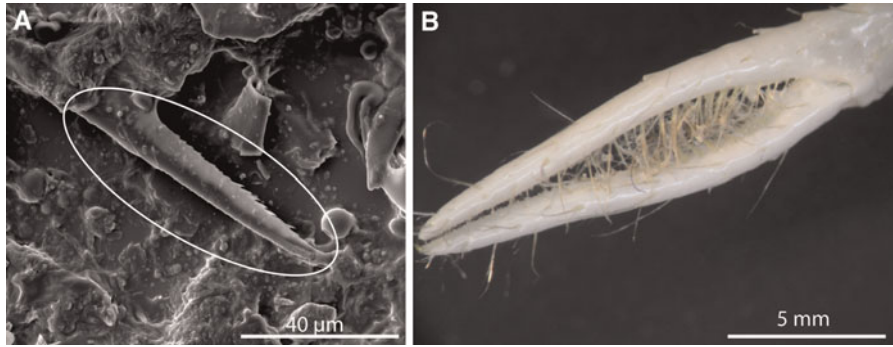


Fig. 4. (A) Stomach contents of *Gastroptychus formosus* in SEM ($\times 3000$) showing crustacean exoskeleton parts (circled); (B) right chela of a specimen caught on the shelf slope off Biscay showing bushy setae on dactylus and propodus.

Museum in London. This species is the only north-eastern Atlantic chirostylid that has distinctively long chelipeds. However *G. salvadori*, recently described from the subtropical north-western Atlantic (Rice & Miller, 1991) would be difficult to differentiate from *G. formosus* by video. Nevertheless, the former is reported to live in association with the brisingid starfish *Novodinia antillensis* rather than antipatharians. We were unable to determine the species of *Gastroptychus* observed off Barbados (Figure 2B), as *G. affinis*, *G. salvadori*, *G. spinifer* and the recently described *Gastroptychus meridionalis* (Melo-Fiho & Melo, 2004) all occur in the eastern Atlantic. It is worth noting that *G. salvadori* (Rice & Miller, 1991) closely resembles *G. formosus* (Pohle & Macpherson, 1995) and is described based on a single specimen of an ovigerous female. Similarly, the description of *G. meridionalis* is based on five ovigerous females and males have never been found.

We have extended the known distribution of *G. formosus* to northern parts of Rockall Trough and our chirostylid records from the Mid-Atlantic Ridge close to the Menez Gwen vent system (Figure 2A) are probably *G. formosus* as they had characteristically long, slender chelipeds and small chelae and were living on *Leiopathes* sp. growing on basalt rock at similar depths (800 m) to the populations off the British Isles. Although *G. formosus* has a wide distribution, it still remains to be determined whether its populations differ genetically due to isolation. An analysis of Galatheidae and Chirostylidae in the Pacific indicated that their populations were not genetically isolated, despite being located on geographically isolated seamounts (Samadi *et al.*, 2006). Other deep-sea chirostylids are known to have a wide geographical range in the North Atlantic like *Uroptychus nitidus* (Zariquiey Álvarez, 1968). More information on the distribution range of all chirostylids

can be found in the recent catalogue of squat lobsters of the world (Baba *et al.*, 2008).

Although *G. formosus* has repeatedly been collected with coral since the first records, their association with coral hosts was not based on *in situ* observations and quantitative data. We have shown that *G. formosus* lives on octocorals and is mainly found on *Leiopathes* sp. which tended to be the bushiest large coral. Note that these colonial corals are not dominant in the studied reefs where scleractinian reef builders cover the main part of the surface (Huvenne *et al.*, 2005). The reasons for this preference are unknown, although *G. formosus* may feed on particulate organic matter and zooplankton trapped in mucus produced by the corals since their stomachs contained minuscule crustacean particles. The chelae of all by-catch and museum individuals examined were characterized by dense comb-like setae on dactylus and propodus (Figure 4B) and it is therefore possible that these chelae are used to brush through coral mucus and collect food particles from nearby coral branches. The feeding could be similar to that of the ophiurid *Astrobrachion constrictum* that lives on the antipatharian *Antipathes fiordensis* in New Zealand fjords where the ophiuroid feeds primarily on mucus produced by the antipatharian polyps as well as on planktonic prey captured by the coral host nematocysts (Grange, 1991). A mutualistic relationship was suggested: the ophiuroid gains protection and food, whilst enhancing the survival of the antipatharian host by cleaning the particulate matter off the polyps and preventing epizoid larval settlement. In shallow water corals, it is already well described how coral mucus provides trapped particles to the heterotrophic reef community (Wild *et al.*, 2004).

During all transects analysed, any *G. formosus* was observed on the reef-builder coral species (i.e. scleractinian corals) and

Table 1. Data on the presence/absence of *Gastroptychus formosus* in relation to host coral types at five sites visited during the 'Caracole' cruise in 2001 (Thérèse Mound, Pelagia Mounds, Logatchev Mounds) and the 'Ark XIX/3' cruise in 2003 (Twin Mounds and Giant Mounds). N_{gfo1} : presence of at least one *G. formosus* on coral, N_{gfo0} : absence of *G. formosus* on coral.

	Thérèse Mound		Pelagia Mounds		Logatchev Mounds		Twin Mounds		Giant Mounds	
	N_{gfo1}	N_{gfo0}	N_{gfo1}	N_{gfo0}	N_{gfo1}	N_{gfo0}	N_{gfo1}	N_{gfo0}	N_{gfo1}	N_{gfo0}
<i>Leiopathes</i> sp.	240	1018	2	19	17	119	16	82	28	380
<i>Bathypathes</i> sp.	0	5	0	7	4	10	2	119	5	53
<i>Paramuricea</i> sp.	21	3376	0	16	1	15	0	2	6	204

Table 2. Slope estimate and Wald-statistic for the logistic regression fitted with presence/absence of *Gastroptychus formosus*. Slope estimate gives the positive or negative effect of the variables (corals and collection sites) on the model, and Wald statistic gives the *P* values associated with each variable.

	Slope estimate	<i>P</i> value
<i>Leiopathes</i> sp.	1.49	<2e-16
<i>Bathypathes</i> sp.	0.62	0.0155
<i>Paramuricea</i> sp.	-2.11	<2e-16
Thérèse Mound	0.63	0.0005
Pelagia Mounds	-0.49	0.4118
Logatchev Mounds	0.31	0.2178
Twin Mounds	-0.04	0.8932
Giant Mounds	-0.41	0.0545

neither they were during close up view of these species. However, as already reported in various deep-sea coral reefs of the north-eastern Atlantic (Mortensen *et al.*, 1995; Kelmanson & Matz, 2003; Jonsson *et al.*, 2004; Roberts *et al.*, 2008), numerous Galatheidae from the genus *Munida* were observed living in the *Lophelia* reef interstices during ROV sampling operations. We suggest that a comparison of the diet of *G. formosus* and *Munida* spp. (*Munida sarsi*, *Munida rugosa* and *Munida intermedia*) including stable isotopic analysis of C¹³ and N¹⁵ from corals and squat lobster tissues respectively could be relevant in the study of the ecology of the squat lobsters living in deep-sea coral reef communities.

CONCLUSION

Chirostylids are typically deep water animals from the continental slope to abyssal depth and often are associated with corals such as antipatharians and gorgonaceans (Baba *et al.*, 2008). In this paper we have updated the known distribution for *G. formosus*, confirming that it is an amphiatlantic species that occurs along the Mid-Atlantic Ridge at least as far south as the Azores and at least as far north as Scotland at depths of 600–1700 m. On deep water corals, the adults have very specific habitat preferences, being only found on antipatharians and gorgonians (soft corals) with a strong preference for the antipatharian *Leiopathes* sp. as a host. This highly restricted habitat preference is likely to render chirostylids vulnerable to the impacts of demersal fishing both directly as by-catch and indirectly through habitat loss. The past 20 years have seen an increased intensity of deep-water fishing in the north-eastern Atlantic which has led to damage to carbonate mound habitats although demersal trawlers try to avoid gear contact with scleractinian coral reefs due to the extensive damage this causes to their gear and their catch (Hall-Spencer *et al.*, 2002). However, antipatharian corals such as *Leiopathes* sp. are frequently found attached to cobbles and boulders on sedimentary grounds that are more accessible by trawlers (Hall-Spencer *et al.*, 2002). These boulders are difficult to detect even with modern echosounder technology, and although not targeted by fishermen, their attached fauna is at high risk of destruction through accidental trawling (Davies *et al.*, 2007). We are only beginning to understand the basic ecology of deep coral habitats but there is clearly a need for improved management of these systems to protect long-lived corals and their associated species.

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