Lionfish (*Pterois spp.*) invade the upper-bathyal zone in the western Atlantic

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Non-native lionfish have been recorded throughout the western Atlantic on both shallow and mesophotic reefs, where they have been linked to declines in reef health. In this study we report the first lionfish observations from the deep sea (>200 m) in Bermuda and Roatan, Honduras, with lionfish observed to a maximum depth of 304 m off the Bermuda platform, and 250 m off West End, Roatan. Placed in the context of other deeper lionfish observations and records, our results imply that lionfish may be present in the 200-300 m depth range of the upper-bathyal zone across many locations in the western Atlantic, but currently are under-sampled compared to shallow habitats. We highlight the need for considering deep-sea lionfish populations in future invasive lionfish management.

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21   **Abstract**

22   Non-native lionfish have been recorded throughout the western Atlantic on both shallow and

23   mesophotic reefs, where they have been linked to declines in reef health. In this study we report

24   the first lionfish observations from the deep sea (>200 m) in Bermuda and Roatan, Honduras,

25   with lionfish observed to a maximum depth of 304 m off the Bermuda platform, and 250 m off

26   West End, Roatan. Placed in the context of other deeper lionfish observations and records, our

27   results imply that lionfish may be present in the 200-300 m depth range of the upper-bathyal

28   zone across many locations in the western Atlantic, but currently are under-sampled compared to

29   shallow habitats. We highlight the need for considering deep-sea lionfish populations in future

30   invasive lionfish management.

31   **Introduction**

32

33   Non-native lionfish, first documented in the western Atlantic region in the 1980s (Schofield,

34   2009; 2010), are considered a major threat to western Atlantic reef communities (Sutherland et

35   al., 2010). Lionfish are benthic generalist predators, and their presence on shallow coral reefs has

36   been associated with up to 65% decline in their prey fish biomass (Green et al., 2012), leading to

37   overall declines in fish recruitment of up to 79% (Albins & Hixon, 2008). In some cases lionfish

38   have been observed to feed on critically-endangered reef fish (Rocha et al., 2015). On both

39   shallow reefs and mesophotic coral ecosystems (MCEs, reefs from 30 to approximately 150-180

40   m depth; Hinderstein et al., 2010), non-native lionfish are thought to cause increased algal cover

41   by consuming herbivores and causing trophic cascades (Lesser & Slattery, 2011; Slattery &

42   Lesser, 2014; Kindinger & Albins, 2017). Native to the Indian and Pacific oceans and Red Sea,

43   lionfish in the western Atlantic have now been recorded from New York, USA in the north

44   (Meister et al., 2005), to as far south as the southeastern coast of Brazil (Ferreira et al., 2015). In

45   addition, there is a second lionfish invasion currently underway in the Mediterranean Sea (Kletou,

46   Hall-Spencer & Kleitou, 2016). Two species of non-native lionfish have been recorded in the

47   western Atlantic: *Pterois volitans* (Linnaeus, 1758) and *P. miles* (Bennett, 1828) (Hamner et al.,

48   2007), though they are believed to be ecologically synonymous in their impacts to western

49   Atlantic marine communities (Morris et al., 2009).

50   The majority of research on lionfish invasions has focused on shallow coral reefs (<30 m),

51   mangroves and seagrass beds (Morris et al., 2009; Claydon, Calosso & Traiger, 2012). However,

52   recent studies have highlighted their widespread presence on MCEs across the western Atlantic

53   invaded range (Andradi-Brown et al., 2017a), which is unsurprising, as they have been recorded

54 on MCEs in many locations in their native range. For example, *P. miles* at 65 m in the Red Sea

55 (Brokovich et al. 2008), and *P. volitans* at 75 m in New Caledonia (Kulbicki et al. 2012), 61 m in

56 Micronesia (Andradi-Brown et al. 2017a), 61 m in the Philippines (Andradi-Brown et al. 2017a),

57 and at 80 m in American Samoa (Wright 2005). With two exceptions (see next paragraph),

58 MCEs represent the deepest depths lionfish have been previously reported from locations across

59 the western Atlantic. For example, from remote operated vehicle (ROV) surveys: 112 m in the

60 northwestern Gulf of Mexico (Nuttall et al., 2014), 100 m off North Carolina, USA (Meister et

61 al., 2005), 126 m on the Desecheo Ridge west of Puerto Rico (Quattrini et al., 2017), and 167 m

62 on the Conrad Seamount in the Anegada Passage (Quattrini et al., 2017). Lionfish have also been

63 observed at 120 m from submersible dives in Honduras (Schofield, 2010), and collected from

64 trawl surveys >80 m depth in the eastern Gulf of Mexico (Switzer et al., 2015). In addition,

65 diver-based surveys on MCEs have reported sightings in the 30-100 m range in Puerto Rico

66 (Bejarano, Appeldoorn & Nemeth, 2014), Bermuda (Pinheiro et al., 2016), and the Lesser

67 Antilles (de León et al., 2013). Therefore, it has been suggested that lionfish have widely

68 colonised MCEs across the western Atlantic (Andradi-Brown et al., 2017a).

69   In August 2010, while conducting submersible surveys off Lyford Cay, Nassau, The

70 Bahamas, lionfish were observed at 300 m (pers. comm. from R.G. Gilmore in: Albins & Hixon,

71 2013; McGuire & Hill, 2014). While in Curaçao, the *Curasub* has reported observing lionfish

72 regularly down to 247 m depth (Tornabene & Baldwin, 2017). To our knowledge these sightings

73 represent the maximum known depth distribution of lionfish in the western Atlantic, and the only

74 records of lionfish in the deep sea (defined as >200 m depth; Rogers, 2015). It is not clear

75 whether this sighting represents an isolated incident of a lionfish reaching these depths, or

76 whether lionfish more regularly use habitats in the >200 m depth range, but they have not

77 previously been recorded because of limited surveys within this depth range.

78   In this study we report visual observations of lionfish >200 m depth in two new locations

79 within the western Atlantic region: Bermuda and Roatan, Honduras. We also consider other

80 lionfish records that could potentially indicate that lionfish may be more widespread at >200 m

81 depth across the western Atlantic range.

82

83 **Methods**

84

85 Bermuda is a series of islands located far off the continental shelf in the northwestern Sargasso

86 Sea (Fig 1A). The islands exist on a large shallow-water platform (approximately 20 m depth,

87 623 km^2 area) which are the eroded remains of a Meso-Cenozoic volcanic peak (Coates et al.,

88 2013). The platform is surrounded by a shallow slope, which transitions into near-vertical walls

89 at around 100 m (Coates et al., 2013). While deep reef areas of Bermuda are poorly studied, with

90 few observations below mesophotic depths, there are established MCE communities around

91 Bermuda to at least 80 m (Pinheiro et al., 2016). MCE to deep-sea benthic organisms and

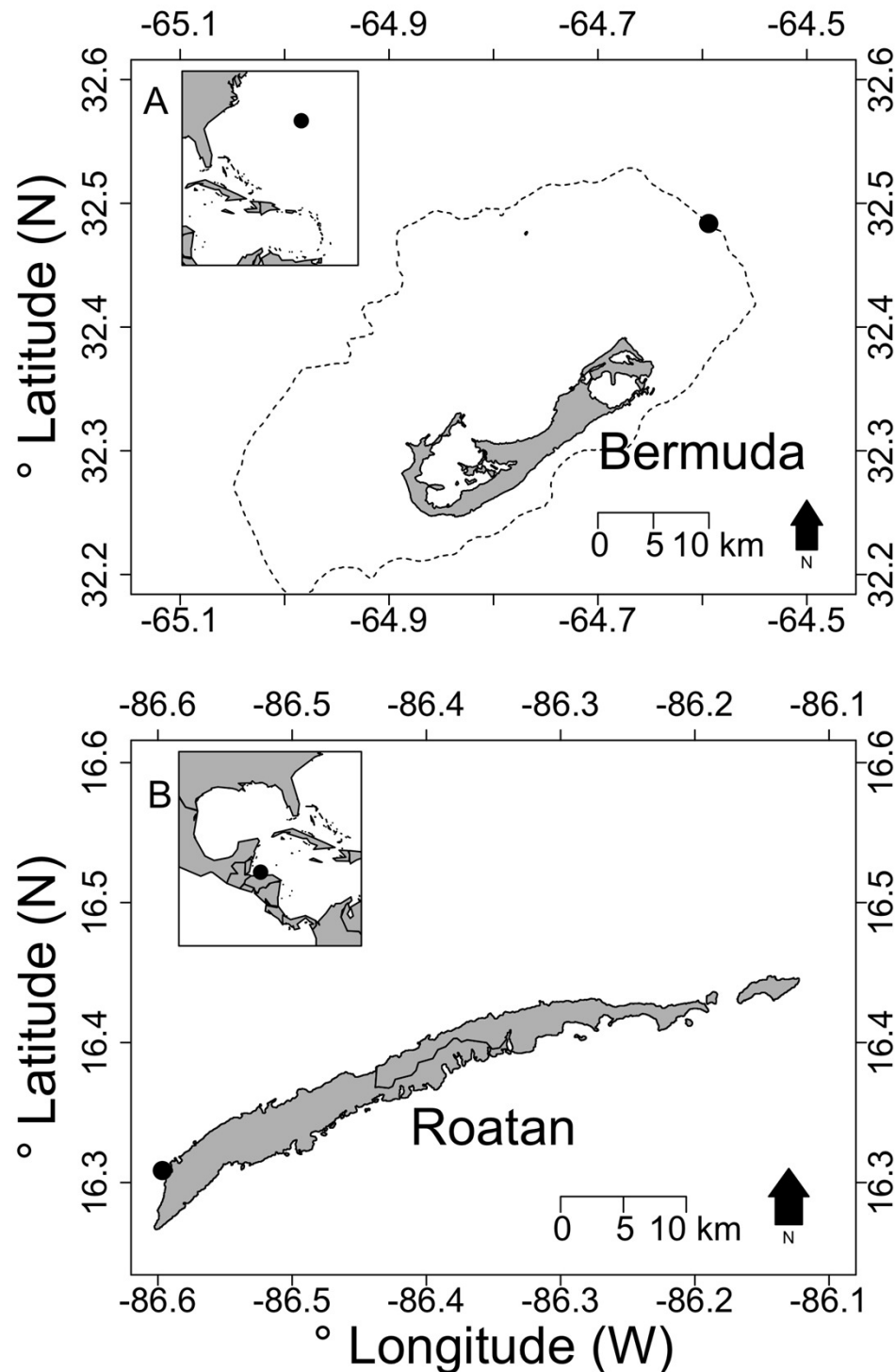
92 benthic-associated fish surveys were undertaken during daylight hours using the *Nemo* and

93 *Nomad* Triton 1000-2 class submersibles (Vero Beach, Florida, USA) down to 300 m depth

94 around the edge of the Bermuda platform during July and August 2016 as part of the Nekton

95 Foundation/XL-Catlin Deep-Ocean Survey – Mission 1 (www.nektonmission.org). In total, 17

96 dives were conducted to 300 m between both submersibles. Research permits for Bermuda were

97 issued by the Department of Environment and Natural Resources, Bermuda (No. 2016070751).

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99   Figure 1. Map showing location of deepest observed lionfish for (A) Bermuda and (B) Roatan,

100   Honduras. Inset maps indicate the locations of Bermuda and Roatan respectively relative to the

101   western Atlantic region. In (A) the dashed line indicates the 50 m depth contour to show the

102   outline of the Bermuda platform. The reef drops off steeply at this location, such that our 304 m

103   lionfish observation is close to the 50 m depth contour.

104

105   In contrast, Roatan is an island in the Caribbean Sea located off the north coast of

106   mainland Honduras (Fig 1B). Roatan is approximately 50 km long and 2-4 km wide, and has a

107   total land area of about 200 km^2. This island is surrounded by shallow fringing coral reefs, which

108   transition into MCEs at increased depths. The Roatan Institute of Deepsea Exploration conducts

109   commercial submarine tourism, using the *Idabel* submarine allowing tourists to observe deep-sea

110   habitats to 610 m depth. With year-round operations from Half Moon Bay, West End, Roatan,

111   *Idabel* conducted 224 dives ≥300 m between Jan 2015–April 2017. During March 2017 visual

112   observations of benthic communities and their associated fish communities were conducted on a

113   night dive to 300 m depth. Visual/video lionfish observations in Roatan were covered under the

114   Roatan Institute of Deepsea Exploration operating permit issued by the Municipalidad de Roatan

115   (No. 1391).

116   To identify other records of deep lionfish we examined 6,814 lionfish records from the

117   US Geological Survey Nonindigenous Aquatic Species database (USGS-NAS, 2017). Lionfish

118   records in the database have been gathered from media reports, scientific publications and direct

119   reports to the database managers. All records contain a GPS location, and in some cases a short

120   description of the conditions under which the lionfish was observed and/or a photo of the lionfish.

121   In some cases the descriptions accompanying records included depth information, though this is

122   not formatted in a consistent way (for example using different units such as metres, feet,

123   fathoms) and contained within a larger text record description. We initially viewed these

124   descriptions to identify any records directly stating lionfish observations at depths ≥200 m,

125 converting any depth information provided into metres for consideration. To further identify

126 potential lionfish records from ≥200 m depth, we downloaded the 2014 General Bathymetric

127 Chart of the Oceans (http://www.gebco.net) 30 arc-second interval grid bathymetry for the

128 western Atlantic region. We used the raster package (Hijmans, 2015) in R (R Core Team, 2013)

129 to identify approximate depths of all lionfish records based on GPS location. All records

130 associated with bathymetry ≥200 m depth were individually reviewed and classified as potential

131 deep-sea individuals, or excluded. Records were excluded for any of the following reasons: (i)

132 specific depth information was available in the record indicating the fish was <200 m depth, (ii)

133 the record reports that the observation was made by a diver or snorkeler, (iii) the location of the

134 record is a well known/established shallow reef diving/snorkelling site, or (iv) the lionfish were

135 collected by hook-and-line making it highly unlikely they were from ≥200 m depth. Raw data are

136 available from the US Geological Survey Nonindigenous Aquatic Species database (USGS-NAS,

137 2017), and ESM1 contains a list of all lionfish GPS locations present in the database at the time

138 of analysis that were used in this study. ESM2 contains the raw R code used to assign a depth to

139 each lionfish record.

140

141 **Results**

142

143 In Bermuda during daytime dives on 28 July 2016 off the northeastern edge of the Bermuda

144 platform at 32.483683 N, 64.59395 W (Fig 1A; GPS coordinates in WGS84 format), multiple

145 lionfish were observed. The deepest lionfish were a single individual observed at 304 m depth,

146 and another individual at 297 m (Fig 2). Water temperature was recorded on the submersible

147   during the dive as 19.7 °C at 300 m. The laser points in Fig 2B are 0.25 m apart, suggesting an

148   approximate total length of 21 cm for this individual at 297 m.

149   In Roatan, on 11 March 2017 off Half Moon Bay, West End at 16.308565 N, 86.596681

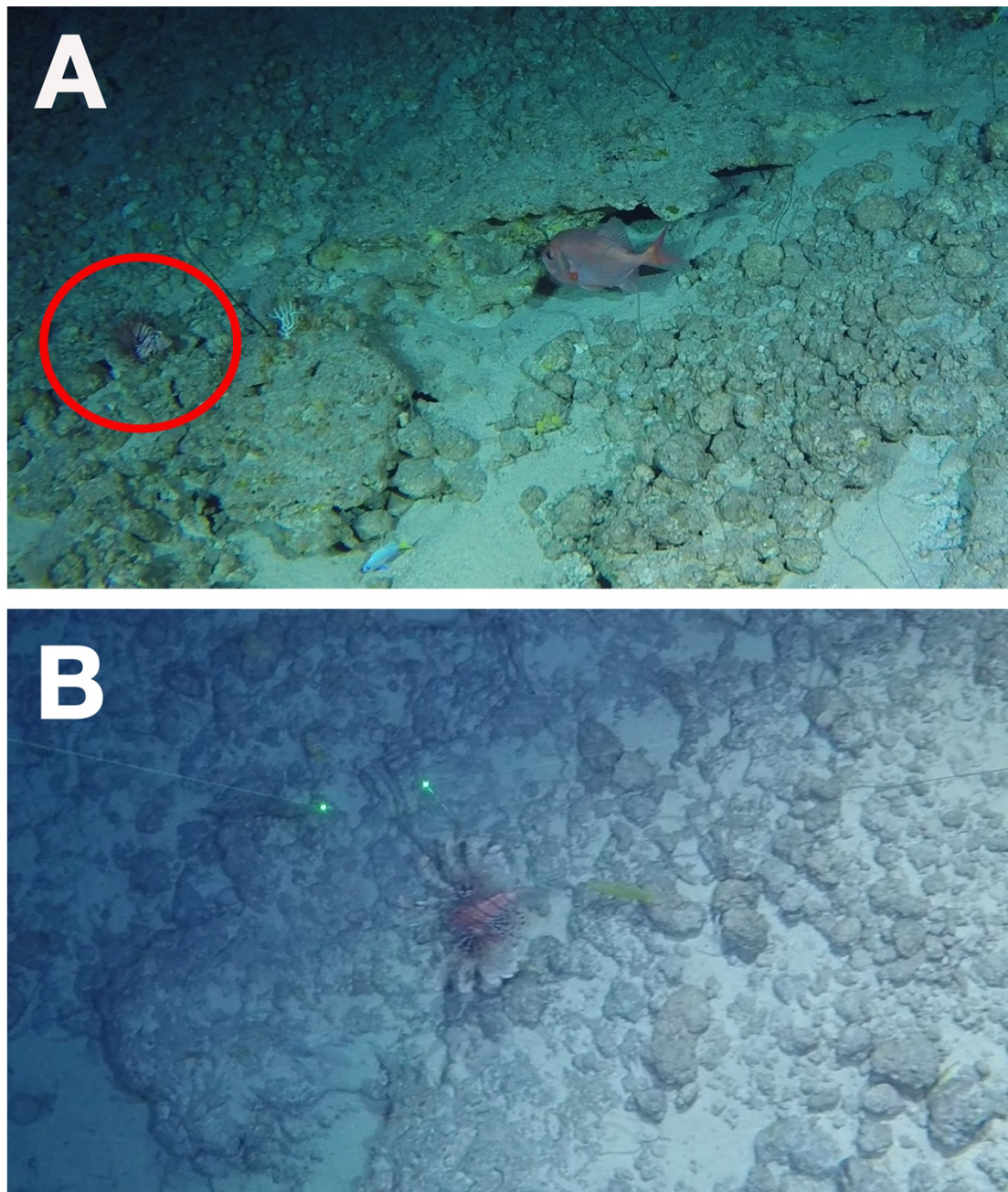
150   W (Fig 1B) five lionfish were observed and photographed down to a depth of 240 m (Fig 3).

151   Individuals were seen in on lower-MCEs (180 m; Fig 3A), and the upper-bathyal (240 m; Fig

152   3B). Water temperature was recorded on this dive as approximately 15 °C at 240 m. However,

153   with year-round tourist submarine dives operating from Half Moon Bay visiting deep reef

154   habitats ≥300 m (224 dives between Jan 2015–April 2017), the *Idabel* has regularly observed

155   lionfish to a maximum depth of 250 m.

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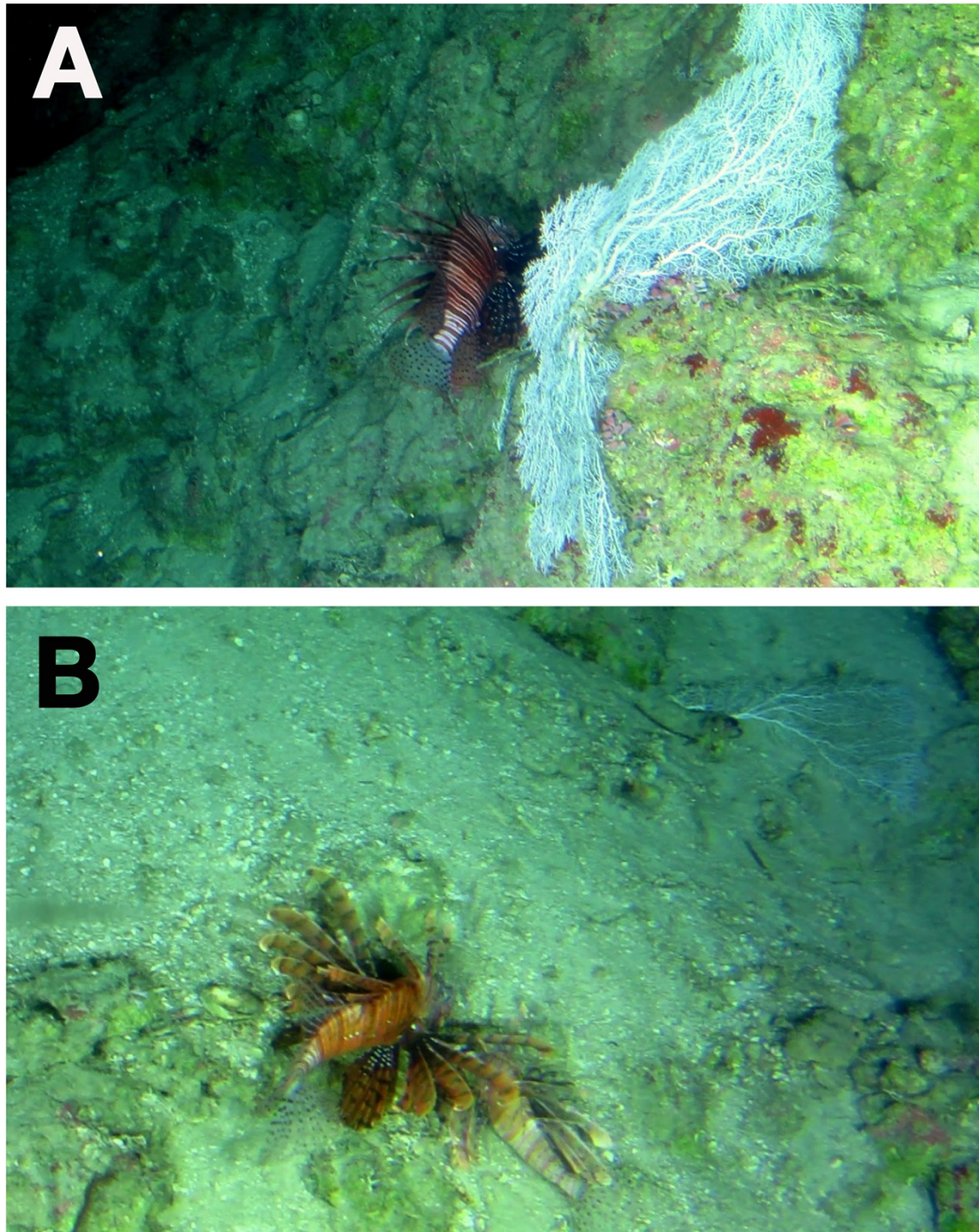
157   Figure 2. Lionfish at 297 m depth off the northeastern slope of the Bermuda platform. (A) The

158   lionfish resting on the reef is indicated within the red circle. Other fish species shown are

159   *Gephyroberyx darwinii* and cf. *Pronotogrammus martinicensis*. (B) Lionfish swimming over the

160   benthos. The laser dots are separated by 0.25 m. Both (A) and (B) show the same individual that

161   swam across the benthos as disturbed by the submersible.

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163   Figure 3. Lionfish off Half Moon Bay, West End, Roatan, Honduras. (A) Lionfish swimming

164   over the benthos at 180 m depth, and (B) two lionfish resting at 240 m depth.

165   When analysing records from the US Geological Survey Nonindigenous Aquatic Species

166   database, no records were found explicitly stating a depth of observation ≥200 m. However, 186

167   records out of the 6,814 records were associated with bathymetry ≥200 m. Of these, after

168   scrutinising the text descriptions, we excluded 185 records as being too shallow. Many of these

169   records represented sites with steep walls spanning from shallow reefs to >200 m depth, and

170   while the resolution of the available bathymetry suggested these were ≥200m, when checking the

171   associated meta-data for these 185 records it clearly indicated that the lionfish were most-likely

172   <200 m. The one record that we retained did not contain enough detail to confirm or reject it as a

173   sighting from >200m. Figure 4 shows the locations of this unconfirmed record, the previously

174   confirmed 300 m lionfish observation in the Bahamas (Albins & Hixon, 2013; McGuire & Hill,

175   2014), the recorded observations in Curaçao at 247 m (Tornabene & Baldwin, 2017), and the

176   locations of our deep-sea lionfish observations in Bermuda and Roatan. We have now added our

177   new deep-sea lionfish observations to the US Geological Survey Nonindigenous Aquatic Species

178   database.

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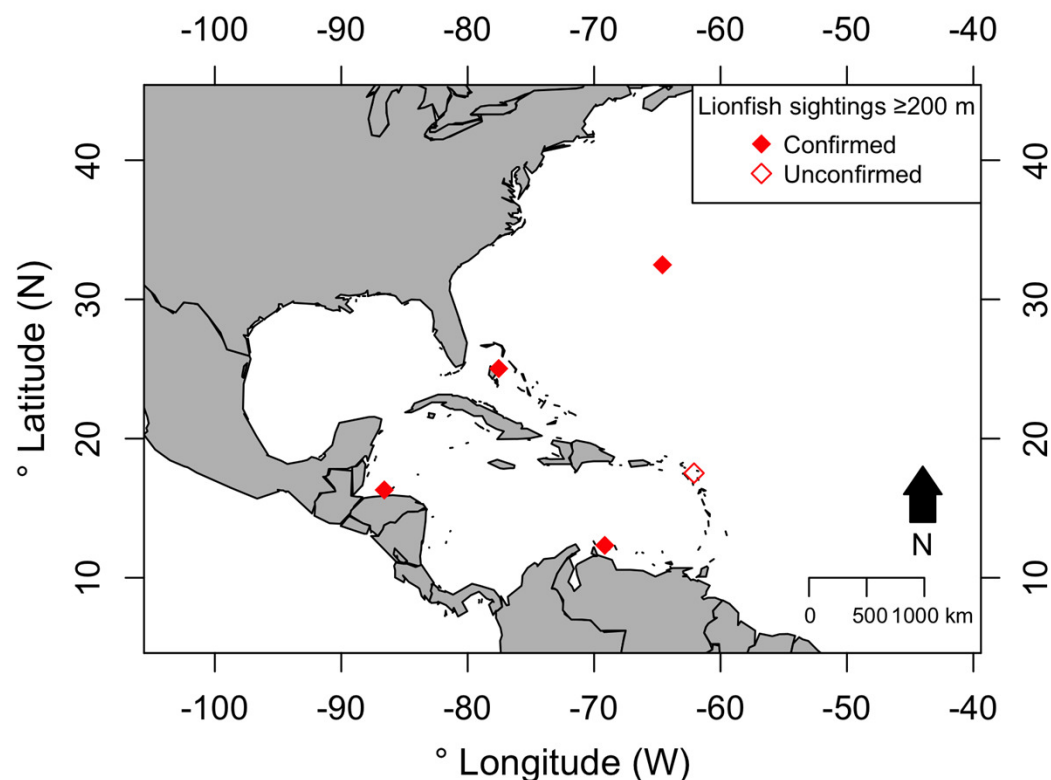
180 Figure 4. Locations of confirmed and possible lionfish observations ≥200 m depth in the western

181 Atlantic. The confirmed sightings represent our observations in Bermuda and Roatan, and the

182 previously reported observations in the Bahamas (Albins & Hixon, 2013) and Curaçao

183 (Tornabene & Baldwin, 2017). The unconfirmed sighting represent a record from the US

184 Geological Survey Nonindigenous Aquatic Species database associated with bathymetry ≥200 m,

185 though there is no direct information on the depth of the lionfish observation for this record.

186

187 **Discussion**

188

189 In this study we report deep-sea lionfish observations from the upper-bathyal zone in two new

190 locations within the invaded western Atlantic lionfish range. Both in Bermuda, close to the

191 northern limit of the lionfish overwintering invaded range (Eddy et al., 2016), and in Roatan,

192   within the centre of the lionfish invaded range (Schofield, 2010), we report lionfish >200 m

193   depth. Because of the large geographical distance between our observations, combined with the

194   previous confirmed observations of lionfish >200 m from the Bahamas (pers. comm. from R.G.

195   Gilmore in: Albins & Hixon, 2013) and Curaçao (Tornabene & Baldwin, 2017), we suggest that

196   lionfish may be more widespread and common than presently understood in deep-sea habitats in

197   the 200-300 m depth range and that this deeper aspect of the lionfish invasion has likely been

198   under-sampled.

199   When searching the US Geological Survey Nonindigenous Aquatic Species database, we

200   found one lionfish record located over bathymetry ≥200 m without stating a depth or giving any

201   indication of depth. While the US Geological Survey Nonindigenous Aquatic Species records

202   have been placed over bathymetry in previous studies, leading to the suggestion that lionfish may

203   extend their maximum depth to 610 m (Johnston & Purkis, 2011), our results indicate depth

204   records generated in this way must be treated with caution. The grid resolution of bathymetry

205   available at a regional level is not sufficient to generate precise lionfish depth information over

206   undersea structures such as walls and steep slopes, where large differences in depth occur within

207   one raster grid square. For this reason, despite identifying 186 records associated with deeper

208   bathymetry, 185 of these were excluded for containing either specific depth details or enough

209   information to suggest that they were most likely shallower reef or MCE observations. Some of

210   these excluded observations were from lionfish associated with oil and gas rigs, where lionfish

211   were associated with the rig structure at shallower depths rather than actually with seabed

212   benthic habitats. Therefore, from simply matching GPS locations with bathymetry, these records

213   would appear to be >200 m and far from any shallower habitat, yet they actually represent

214   shallower lionfish. As many of these records in the US Geological Survey Nonindigenous

215   Aquatic Species database come from recreational and scientific divers and fisheries, we would

216   expect these records to be biased towards shallow reefs where the majority of sampling has

217   occurred. Therefore, it was not surprising that 6628 of the 6814 records were associated with

218   shallow reef or MCE bathymetry. With this biased survey effort to the shallows, the lack of

219   records >200 m in the database should be treated as an indication of under-sampling at depth,

220   and not that lionfish are not present in the upper-bathyal.

221   It is not clear why differences in the maximum depth of observations exist between Roatan,

222   our observations in Bermuda and previous observations in the Bahamas and Curaçao. While in

223   Bermuda we observed lionfish to the maximum survey depth (304 m), in Roatan, despite 224

224   submarine dives to ≥300 m over the past 2.3 years, lionfish have not been observed deeper than

225   250 m. There are many possible explanations related to changing environmental conditions, such

226   as temperature and light, or availability of prey. For example, lionfish are limited by temperature

227   (Whitfield et al., 2014; Dabruzzi, Bennett & Fangue, 2017), with lab experiments suggesting

228   they are unable to survive temperatures <10 °C, but crucially they ceased feeding at temperatures

229   <16.1 °C (Kimball et al., 2004). While detailed temperature data across the depth gradient is not

230   available for the locations we surveyed, water temperature was approximately 15 °C at 240 m in

231   Roatan when we photographed lionfish in March 2017. Therefore, it is possible that the 250 m

232   maximum depth of lionfish observations around Roatan may be caused by temperature limitation.

233   In contrast, water temperature was 19.7 °C in Bermuda at 300 m, above the temperature of

234   feeding cessation for lionfish (Kimball et al., 2004). This suggests that if temperature is the main

235   limiting factor for maximum depth, we may expect lionfish to extend even deeper than 304 m in

236   Bermuda.

237   Other factors such as light could also influence the maximum depth for lionfish. Lionfish are

238   visual predators (Cure et al., 2012); therefore, despite previous studies indicating reef fish have

239   high visual system plasticity to adapt to low light levels at depth (Brokovich et al., 2010), it is

240   likely they will be limited by light. Bermuda has high light penetration (Fricke & Meischner,

241   1985; Coates et al., 2013), while Roatan suffers from higher sedimentation rates (Mehrtens et al.,

242   2001; Harborne, Afzal & Andrews, 2001), likely reducing light penetration to lower levels than

243   Bermuda. Further research is required to understand the ecological and physiological constraints

244   on maximum lionfish depths.

245   Little is known about the potential impacts of invasive lionfish on the upper-bathyal zone.

246   However, shallow reef research has suggested large declines in native reef fish abundance and

247   recruitment are caused by lionfish (Albins & Hixon, 2008; Green et al., 2012). Shallow reef fish

248   species generally have higher individual and population growth rates when compared to deep sea

249   fish species (Rogers, 1994; Norse et al., 2012). Therefore, predation by lionfish may have greater

250   potential for damage to native fish communities in the upper-bathyal zone. With so few records

251   of bathyal lionfish and no quantitative estimates of lionfish densities, the ecological impacts at

252   >200 m depth is unknown.

253   Current lionfish management is highly biased towards shallow reef habitats, with diver-

254   conducted culling the major control measure implemented in the western Atlantic (Morris et al.,

255   2009). While shallow reef culling has been found to reduce lionfish densities (Frazer et al., 2012)

256   and help native fish populations recover (Green et al., 2014), a recent study has suggested strong

257   depth-specific effects of culling on lionfish densities, with substantial lionfish populations

258   remaining on MCEs despite shallow culling (Andradi-Brown et al., 2017b). Previous modelling

259   studies have highlighted that substantial deep refuges for lionfish have the potential to undermine

260   current management programmes (Arias-González et al., 2011). Therefore, if lionfish are

261   widespread in the 200-300 m depth range across the western Atlantic this raises further

262   challenges for lionfish management. There are currently few effective methods for lionfish

263   removal in water too deep for diving, with trapping being the only widely used method. In

264   Bermuda, lobster traps have been used to remove lionfish from MCEs, with trap modifications

265   substantially reducing bycatch of other fish species (Pitt & Trott, 2015). Though measures of

266   trapping effectiveness for reducing deep lionfish populations are still lacking. Traps could be

267   trialled deeper for lionfish control in the 200-300 m range, and cameras used to monitor effects

268   on lionfish densities.

269   This study documents non-native lionfish in the upper-bathyal zone in Bermuda, and Roatan,

270   Honduras for the first time. Our observations, combined with other lionfish records, suggest that

271   lionfish could potentially be present in 200-300 m depth habitat in many locations in the western

272   Atlantic. Further surveys should be conducted to assess how widely lionfish are using upper-

273   bathyal habitats, and to establish their population densities. Our results highlight the need to

274   consider deeper lionfish populations in management programmes.

275

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283 or firm names is for descriptive purposes only and does not imply endorsement by the US

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