

# Meristic variation in males of the hydrothermal vent octopus, *Muusoctopus hydrothermalis* (Cephalopoda: Octopodidae)

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*Intraspecific variation in characters such as arm sucker and gill lamellae counts in octopodids is yet to be thoroughly investigated, potentially hampering our ability to recognize species. In this study, data from 13 specimens of Muusoctopus hydrothermalis collected at four hydrothermal vents on the East Pacific Rise between 8°38'N and 12°48'N are considered. Although the northern and southern octopuses differ minimally in size, mean sucker count by arm in the northern group is 11.7 to 22.8% higher than it is in the southern group; in addition these octopuses typically have an additional gill lamella and bulkier funnel organs. The arms of each individual carry a different number of suckers. The difference is significant on nonadjacent arms, a pattern that merits examination in a broader taxonomic context. Why these differences exist among conspecifics remains unknown, the incidence of parasitic copepods is not different between the groups and the between-group variation in arm suckers seen here compares well with a previous report of variation among 18 specimens from the type locality. Increases in meristic characters (counts) in fish are attributed to lower temperatures during embryonic development following Jordan's rule. Northern and southern vents offer the octopuses a wide temperature range, but vent fluid chemistry differs. Northern vent fluids may be more toxic; if so, developing octopus embryos may survive only minimal vent fluid exposure and therefore develop at low temperatures. At the less toxic southern vents, eggs may survive greater exposure to vent fluids and thus develop at higher temperatures.*

**Keywords:** arm sucker counts, gill lamellae, population variation, funnel organ, hectocotylized arm suckers, Jordan's rule

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## INTRODUCTION

Long bemoaned in the literature, the magnitude of morphological variation among conspecific specimens of octopuses has rarely been quantified (Allcock *et al.*, 2008). Although net preservation-linked deformation is minimal in the uniformly muscular bodies of shallow-water octopodid specimens (Voight, 1991), specimens of the deep-sea octopus genus *Graneledone* have a fluid-rich layer. Measurements of these specimens change during long-term storage in ethanol (Voight, 2001). To minimize real and perceived problems with measurements, meristic characters or serial counts of body elements (O'Reilly & Horn, 2004), such as gill lamellae and arm suckers, have become standard in species descriptions. These meristic characters should be unaffected by preservation artefact, but the extent of their variation remains nearly unexplored in cephalopods and in molluscs generally.

González & Guerra, 1998 (in González *et al.*, 1998) described a distinctive species, *Vulcanoctopus hydrothermalis*, from the hydrothermal vent Genesis at 12°48.43'N 103°56.41'W on the East Pacific Rise. Male specimens that

have received study were exclusively collected in this area (González *et al.*, 2002), although the species is documented at several areas of hydrothermal activity on the ridge crest and ranges from at least 13°N to 23°S (González *et al.*, 2006). In its unusual habitat, the octopus feeds on swarming amphipods (Voight, 2005) which often associate with giant tube worms of *Riftia pachyptila* Jones, 1981 that are sustained by hot, metal-rich anoxic fluids. Strugnell *et al.* (2009) demonstrated the species to be nested within the monophyletic genus *Benthooctopus*. Taxonomic issues plaguing that genus name led Gleadall *et al.* (2010) to extend the definition of *Muusoctopus* Gleadall, 2004 to include all species assigned to *Benthooctopus*. They, however, stated that *Vulcanoctopus* although a member of the clade should be retained as distinct, based on the criterion of sufficient difference. As taxonomy is intended to reflect phylogenetic relationships, the species is here assigned to the clade *Muusoctopus*.

To document variation in meristic characters in a single octopodid species, counts and measurements of specimens of *M. hydrothermalis* are considered. Data are from 13 specimens collected between 1994 and 2003 by the Deep Submergence Vehicle (DSV) 'Alvin' from four hydrothermal vents between 8°38'N and 12°48'N on the East Pacific Rise. The variation found here remains enigmatic; it might be linked to genetic differences, or to environment, specifically temperature, following a generality in fish known as Jordan's rule.

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## MATERIALS AND METHODS

Octopuses of *Muusoctopus hydrothermalis* were collected using the suction sampler by the DSV 'Alvin' at from 2495 to 2620 m depths on the East Pacific Rise. One specimen collected at 8°38' N104°13'W and three from 9°50' N104°18'W form the 9°N group; the 13°N group contains one specimen from 10°46' N103°39'W, a new lava flow habitat described by Voight *et al.* (2004), four specimens from Genesis Chimney at 12°48.57'N 103°56.37'W and four from Parigou, a small vent at 12°48.64'N 103°56.42'W, a site described by Voight (2005). Slight differences in position between the site specified here and those in, e.g. González *et al.* (2002) are likely due to different navigational systems.

The Clipperton Fracture Zone forms an east–west offset near 10°N on the otherwise linear ridge, separating these areas (Figure 1). Intraspecific genetic differences in vent taxa from north and south of the fracture zone, including annelids and molluscs, have been sought using allozymes (see review by Jollivet, 1996), DNA sequence data (Won *et al.*, 2003; Hurtado *et al.*, 2004; Matabos *et al.*, 2008) and even microsatellite data (Fusaro, 2008); no significant within-species differences have been detected. Despite the morphological differences reported here, considering these specimens to be conspecific is conservative.

By necessity, collections were *ad hoc*; therefore, the interval between collection of an octopus and its preservation on-board ship likely differed. Specimens were fixed in 8 to 10% buffered formalin in seawater and later transferred to 70% ethanol.

Standard octopodid measurements, as defined by Roper & Voss (1983), were recorded from preserved specimens. Abbreviations are: ML, mantle length; MW, mantle width; HW, head width; AL, arm length, with the roman numerals indicating arm number; AW, arm width (measured at the level of the twentieth sucker on the first right arm); WD, web depth, only the dorsal sector (A) and dorso-lateral (B) sectors are reported; SD, diameter of the largest sucker; FL, funnel length; FFL, free funnel length. Arm length and web depth were measured with a 25 cm rule, features of the mantle, sucker and funnel were measured with electronic callipers. Lengths <10 mm were rounded to the nearest 0.1 mm; others were rounded to the nearest mm. Weights of preserved specimens were determined to the nearest 0.1 g on an electronic scale. Mantle width was measured only after the mantle was opened. Arm suckers and gill lamellae, including the tiny terminal lamella, were counted with the aid of a dissecting microscope. Only the higher count from each arm pair is reported, except counts from both third arms are reported because hectocotylization modifies the third right arm. The mid-ventral funnel was slit longitudinally and the shape of the funnel organ and the state of contraction of the funnel recorded.

To assess whether parasitism by copepods of *Genesis vulcanoptopusi* López-González, Bresciani and Huys, 2000 impacted octopus morphology, the number of copepods in the outer mantle and the inner funnel, including what appear to be scars from previous infections following López-González *et al.* (2000), from the level of the anus to the funnel opening, were counted in each octopus. The total counts were compared between the groups using a Mann–Whitney *U* test.

Data collection revealed that different arm pairs of an individual carry a different number of suckers (Table 1). Whether

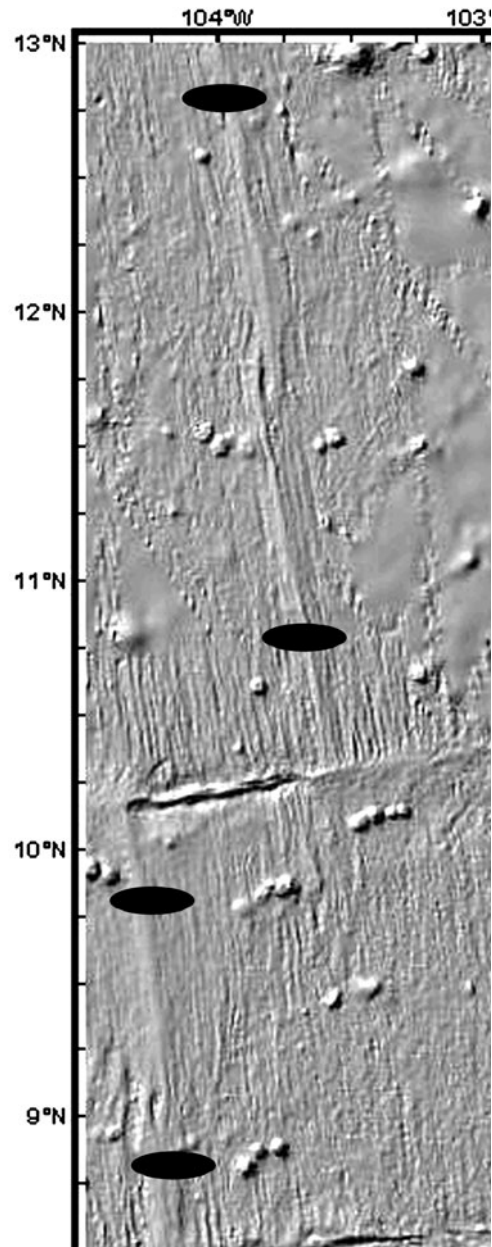


Fig. 1. Map of collection areas (marked by dark oval) on the East Pacific Rise. The Clipperton Fracture Zone is visible as the east–west offset of the ridge at 10°15'N (map modified from Carbotte *et al.*, 2004).

the arm pairs differ significantly in the number of suckers they carry was tested with a Kolmogorov–Smirnov test using pooled data from all specimens. The difference between the greatest and the fewest number of suckers on the arms of each individual were determined. This difference was plotted against the greatest number of suckers on an arm and, in a separate analysis, against arm length. Correlations were calculated to test whether the difference decreased as the number of suckers increased or as the arms lengthened, respectively.

These results are compared to those of González *et al.* (2002) who report the number of suckers per row, with a row being the longitudinal column on the arm for specimens from Genesis, at 12°48.7'N 103°56.43'W. Their counts were doubled prior to comparison.

**Table 1.** Means and ranges for each weight, length and sucker count from specimens from 13°N and 9°N. Weight in g; measurements in mm.

	13°N		9°N	
	N	Mean (range)	N	Mean (range)
Weight	9	34.7 (22.5–47.5)	4	33.9 (20–50.5)
Mantle L	9	47.9 (42–58)	4	48.3 (41–57)
Width	9	27.9 (22–36)	4	29.9 (24–34)
Head width	9	21.2 (17–26)	4	21.8 (20–24)
Sucker diam.	9	2.4 (2–2.6)	4	2.3 (2.1–2.6)
Web depth A	9	27.7 (25–33)	4	27.5 (25–30)
Web depth B	9	26.4 (21–32)	4	28.3 (28–29)
Funnel L	9	10.7 (9.9–12.2)	4	11.3 (7.8–14.3)
Free funnel L	9	4.5 (2.2–6)	4	3.6 (3.4–3.8)
Ligula L	8	6.2 (4.1–7.7)	4	7.4 (6.4–7.9)
Calamus L	8	2.1 (2–3)	4	2.4 (2–3)
Arm				
L I	7	121.7 (103–140)	4	139.3 (123–165)
L II	9	115.2 (100–140)	4	137.3 (112–163)
L III left	8	107.4 (86–126)	2	114.5 (112, 117)
L III right	8	71 (61–83)	4	71.3 (65–80)
L IV	9	104.4 (82–130)	4	110.5 (100–135)
Width	9	5.4 (4.7–6.4)	4	5.2 (3.9–6.1)
Arm sucker counts				
I	7	158.1 (143–166)	3	141.5 (137–153)
II	8	151.4 (137–159)	3	132 (113–149)
III left	8	142.2 (130–155)	2	123 (122, 124)
III right	9	77.1 (75–83)	4	62.8 (58–66)
IV	9	139.6 (127–148)	4	123.3 (115–131)
Gill lamellae	8	9.375/8.625	4	9/8.25

N, number; L, length; diam, diameter; Gill lamellae, mean outer/mean inner counts.

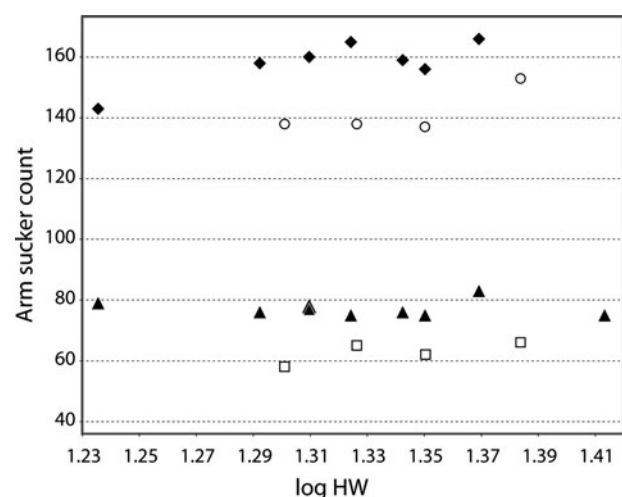
Le Bris *et al.* (2003) reported the chemical composition of hydrothermal vent fluids from Genesis, the collection site of four octopuses reported here (Table 1). The chemical analyses were performed *in situ* using the submersible-mounted chemical analyser Alchemist, during the 'Nautile' cruise Hope '99 (Le Bris *et al.*, 2003). Those and comparable analyses from diverse 9°N vents (Le Bris *et al.*, 2006) serve as proxies of vent fluid toxicity.

## RESULTS

The means and ranges of weights and measurements from the 9°N and 13°N groups are essentially the same (Table 1; original data, supplementary material online), as are the medians (unpublished data). The arms of the 9°N group of four specimens of *Muusoctopus hydrothermalis*, however, have between 11.7 and 22.8% fewer suckers (Figure 2; Table 1) than do the arms of the nine specimens in the 13°N group; the 9°N specimens also have slightly fewer gill lamellae. The differences are not statistically significant and are within the range González *et al.* (2002) report.

In all individuals, different arms carry different numbers of suckers. The difference is significant between nonadjacent, but not between adjacent, arms (Table 2). The difference in the number of suckers carried by the different arms appears consistent regardless of size. The difference between the number of suckers on the arm with the most and with the least suckers is independent of both the greatest number of suckers on one arm of an individual ( $R^2 = 0.0323$ ) and the arm length ( $R^2 = 0.0234$ ).

Variation in arm length relative to mantle size among these 'Alvin'-collected specimens is apparent (Table 1). Specimens collected late in a dive may have been preserved relatively soon after collection, while those collected early in a dive could only have been preserved many hours later. Specimen handling regimes also differed within the 9° group.



**Fig. 2.** Plot of arm sucker count for the first (dorsal) arm pair and the hectocotylus versus log head width. Because variation in arm length artificially enhanced the difference in sucker count, log head width is used here as the x-axis. Solid diamonds are the first arm pair of seven 13°N specimens; solid triangles are the hectocotylus of nine 13°N specimens. Open circles are sucker counts of the dorsal arm pair of four 9°N specimens; open squares are the sucker counts of the hectocotylus of four 9°N specimens.

**Table 2.** Results of the Kolmogorov–Smirnov test for differences in sucker counts on unmodified arms. On diagonal, median number of suckers/number of specimens for each arm, above the diagonal, D statistic; below the diagonal, probability that the difference is significant.

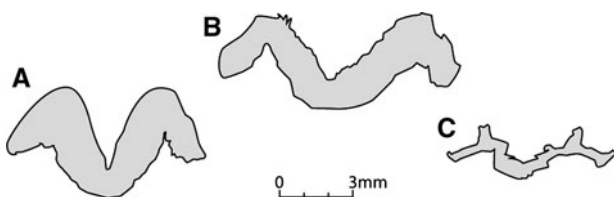
	Arm I	Arm II	Arm III	Arm IV
I	157/10	0.3273	0.600	0.700
II	0.538	150/11	0.5364	0.6364
III	0.031	0.062	141.5/10	0.2692
IV	0.004	0.008	0.736	138/13

González *et al.* (1998) were unable to describe the funnel organ from the type specimen, but the organs are clear in these specimens. The funnel organ of *M. hydrothermalis* is W-shaped with short lateral limbs. Octopuses from 9°N, however, have a thinner, more linear funnel organ than do most specimens from 13°N (Figure 3); variation is present within both groups. Neither the extent of funnel contraction nor mantle collar morphology can be identified as contributing to differences in funnel organ shape. Funnel retraction and blood pooled ventral to the funnel complicated measurements, but both funnel length and free funnel length are independent of head width in the narrow size-range available here ( $R^2 = 0.00003$ ).

Octopuses in the 9°N group carried more copepods and apparent copepod scars than did those in the 13°N group, but the difference was not significant (Table 3;  $U = 29$ ,  $P = 0.106$ ). Octopuses from 9°N have abundant copepods in the funnel but few on the outer mantle; the funnels and mantles of octopuses from 13°N carry about the same number of copepods. The difference in distribution is not significant ( $G = 5.88$ ;  $0.2 > P > 0.10$ ). The number of copepods and their apparent scars ranges in 13°N specimens from zero to 23 (supplementary material online).

## DISCUSSION

Variation in meristic characters appears to be nearly unexplored in molluscs and in cephalopods. Sucker and gill lamellae counts of specimens of *Muusoctopus hydrothermalis* forming the 9°N group are lower by at least 12% than are those forming the 13°N group (Table 1); the funnel organs of the specimens also differ in shape (Figures 2 & 3). González *et al.* (2002) had reported mean sucker counts with standard deviations of up to 16% of the mean of each arm in 18 specimens of the species from Genesis (12°48.7'N 103°56.43'W). Their report of the number of suckers per row that is, the longitudinal column of suckers may have minimized the apparent variation.



**Fig. 3.** Funnel organs of (A) FMNH 307185 (#2) collected at Genesis (12°48.57'N 103°56.37'W) the species type locality; (B) FMNH 307183 collected at 10°46'N 103°39.41'W; (C) FMNH 287366, collected at 9°50'N 104°18'W.

**Table 3.** The number of parasitic copepods in the outer mantle and inner funnel of octopuses from 9°N and 13°N, the latter by site.

	N	Mantle	Funnel
9°N	4	1 ± 1.41	12 ± 2.16
13°N	9	4.2 ± 4.15	3.4 ± 2.96
Genesis	4	5.75 ± 4.86	5 ± 3.56
Parigou	4	1.5 ± 1.29	1.5 ± 1.29

N, number.

The sucker count variation seen here in *M. hydrothermalis* appears to be comparable to the within-species variation shown graphically by Toll (1988) for five octopodid species. Toll (1988) cited differences in arm and hectocotylus sucker counts as characters distinguishing the Atlantic *Scaevargus unircirrhus* (delle Chiaje, 1839) from the Hawaiian *S. patagiatus* Berry, 1913. Norman *et al.* (2005), however, reported only what they perceived to be trivial differences in sucker count between Mediterranean and Pacific specimens of these species. They concluded that Toll examined western Atlantic specimens, and cited his graphical data as evidence that two species of *Scaevargus* exist in the Atlantic Ocean. This study cautions that differences in arm sucker counts, even of over 15%, do not necessarily distinguish species.

Genetic variation might impact sucker number variation. In fish, however, subtle differences in meristic characters, such as the number of vertebrae, correlate with latitude and are attributed to differences in temperature. A generality termed 'Jordan's rule' (Jordan, 1892; McDowall, 2008 and many others) states that lower temperatures, especially during development, increase counts of meristic features (e.g. Hubbs, 1922; Täning, 1952; Lindsey & Harrington, 1972).

Given the broad range of temperatures at hydrothermal vents, these mobile vent-endemic octopuses would presumably select an optimal temperature for egg development, if temperature were the primary environmental variable. Hydrothermal fluid analyses, however, demonstrate that chemically the fluids can differ substantially (Le Bris *et al.*, 2006). Vent fluids at 13°N at Genesis have been shown to be anomalously low in iron, which results in abundant highly toxic hydrogen sulphide (Le Bris *et al.*, 2003). The hydrothermal fluids at most 9°N vents carry more dissolved iron which binds to sulphide to form the much less toxic iron sulphide (Le Bris *et al.*, 2003). If fluids high in hydrogen sulphide are toxic to the octopuses, and no available data suggest octopuses of *M. hydrothermalis* tolerate sulphide exposure, to survive in areas with low iron, eggs would have to develop away from vent fluids, at lower temperatures. In contrast, in areas such as 9°N where vent fluids generally carry more iron and are therefore less toxic (Le Bris *et al.*, 2006), developing eggs might tolerate modest exposure to warm fluids. Jordan's rule predicts that if embryos at Genesis in the 13°N area develop in lower temperatures resultant individuals would have higher counts for both suckers and gill lamellae, consistent with the available data (Table 1).

Unique to this study is the demonstration that an octopus' four arm pairs carry different numbers of suckers (Table 2). All non-hectocotylized arms of shallow-water octopuses tend to carry the same number of suckers (unpublished data), so that the mean count from all intact arms conveys the same information as the count from any one intact arm (Toll, 1988). Because performing counts is time-intensive

and results in minimal variation, often only the suckers of one arm and the hectocotylus are reported; differences among arm pairs in other taxa may exist undiscovered.

Lopez-González *et al.* (2000) suggested that octopuses may encounter swarms of infective stages of copepods of *Genesis vulcanoctopusi*, consistent with the high variation in parasite incidence seen here. Why the copepods occur primarily inside the funnels of octopuses from 9°N and on the outer mantles of those from 13°N remains enigmatic. Although copepod infection elicits host tissue response (Lopez-González *et al.*, 2000) the morphological differences in counts identified here cannot be attributed to the stress of exceedingly heavy parasite loads.

Variation in funnel organ morphology has been noted in several octopodids (five species of *Bathypolypus* by Muus (2002), nine species of *Pareledone* by Allcock (2005) and Allcock *et al.* (2007), two species of *Graneledone* by Voss & Percy (1990) and Allcock *et al.* (2003), two species of *Muusoctopus* by Voss & Percy (1990) and Allcock *et al.* (2006) and in *Ameloctopus litoralis* by Norman (1992)); all of these except the species of *Pareledone* also lack the ink sac. Species of *Pareledone* occur in a seasonally dark Antarctic habitat that may limit the effectiveness of the ink sac. This pattern supports Norman's (1992) suggestion that the funnel organ might be reduced in species lacking an ink sac, and Young & Mangold's (2000) hypothesis that funnel organ secretions are important in forming ink masses that distract visual predators. Apparently without the ink sac, the funnel organ is freer to vary in shape, a potential liability for using this character to diagnose species of deep-sea octopodids. However, the differences in funnel-dwelling copepods may enhance any innate differences in this species.

The variation in arm sucker count seen in this unique hydrothermal vent octopus cautions against undue reliance on this character in species delineation. The parallel changes in gill lamellae and arm suckers suggest a single factor could be responsible for the variation seen. If the eggs that survived developed in different temperatures, these observations are consistent with Jordan's rule; additional data are required to test that hypothesis.

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## Supplementary materials and methods

The Supplementary material referred to in this article can be found online at [journals.cambridge.org/mbi](http://journals.cambridge.org/mbi).

## REFERENCES

- Allcock A.L. (2005) On the confusion surrounding *Pareledone charcoti* (Joubin, 1905) (Cephalopoda: Octopodidae): endemic radiation in the Southern Ocean. *Zoological Journal of the Linnean Society* 143, 75–108.
- Allcock A.L., Collins M.A. and Vecchione M. (2003) A redescription of *Graneledone verrucosa* (Verrill, 1881) (Octopoda: Octopodidae). *Journal of Molluscan Studies* 69, 135–143.
- Allcock A.L., Strugnell J.M., Ruggiero J. and Collins M.A. (2006) Redescription of the deep-sea octopod *Benthooctopus normani* (Massy 1907) and a description of a new species from the Northeast Atlantic. *Marine Biology Research* 2, 372–387.
- Allcock A.L., Strugnell J.M., Prodöhl P., Piatkowski U. and Vecchione M. (2007) A new species of *Pareledone* (Cephalopoda: Octopodidae) from Antarctic Peninsula waters. *Polar Biology* 30, 883–893.
- Allcock A.L., Strugnell J.M. and Johnson M.P. (2008) How useful are the recommended counts and indices in the systematics of the Octopodidae (Mollusca: Cephalopoda)? *Biological Journal of the Linnean Society* 95, 205–218.
- Carbotte S.M., Arko R., Chayes D.N., Haxby W., Lehnert K., O'Hara S., Ryan W.B.F., Weissel R.A., Shipley T., Gahagan L., Johnson K. and Shank T. (2004) New integrated data management system for Ridge2000 and MARGINS research. *Eos Transactions of the American Geophysical Union* 85, 553, doi:10.1029/2004EO510002.
- Fusaro A.J. (2008) *Spatial and temporal population genetics at deep-sea hydrothermal vents along the East Pacific Rise and Galápagos Rift*. PhD thesis. Massachusetts Institute of Technology, Cambridge, USA.
- Gleadall I.G., Guerrero-Kommritz J., Hochberg F.G. Jr and Laptikhovskiy V.L. (2010) The inkless octopuses (Cephalopoda: Octopodidae) of the southwest Atlantic. *Zoological Science* 27, 528–553.
- González A.F., Guerra A., Pascual S. and Briand P. (1998) *Vulcanoctopus hydrothermalis* gen. et sp. nov. (Mollusca, Cephalopoda): an octopod from a deep-sea hydrothermal vent site. *Cahiers Biologie Marine* 39, 169–184.
- González A.F., Guerra A., Rocha F. and Briand P. (2002) Morphological variation in males of *Vulcanoctopus hydrothermalis* (Mollusca, Cephalopoda). *Bulletin of Marine Science* 71, 289–298.
- González A.F., Guerra A. and Segonzac M. (2006). *Vulcanoctopus hydrothermalis*. *Densia* 18, 170.
- Hubbs C.L. (1922) Variations in the number of vertebrae and other meristic characters of fishes correlated with the temperature of water during development. *American Naturalist* 56, 360–372.
- Hurtado L.A., Lutz R.A. and Vrijenhoek R.C. (2004) Distinct patterns of genetic differentiation among annelids of eastern Pacific hydrothermal vents. *Molecular Ecology* 13, 2603–2615.
- Jollivet D. (1996) Specific and genetic diversity at deep-sea hydrothermal vents: an overview. *Biodiversity and Conservation* 5, 1619–1653.
- Jordan D.S. (1892) Relations of temperature to vertebrae among fishes. *Proceedings of the United States National Museum* 1891, 107–120.
- Le Bris N., Sarradin P.-M. and Caprais J.-C. (2003) Contrasted sulphide chemistries in the environment of 13°N EPR vent fauna. *Deep-Sea Research I* 50, 737–747.
- Le Bris N., Govenar B., LeGall C. and Fisher C.R. (2006) Variability of physico-chemical conditions in 9°50'N EPR diffuse flow vent habitats. *Marine Chemistry* 98, 167–182.
- Lindsey C.C. and Harrington R.W. Jr (1972) Extreme vertebral variation induced by temperature in a homozygous clone of the self-fertilizing

- cyprinodontid fish *Rivulus marmoratus*. *Canadian Journal of Zoology* 50, 733–744.
- Lopez- González P.J., Bresciani J., Huys R., González A.F., Guerra A. and Pascual S.** (2000) Description of *Genesis vulcanoctopus* gen. et sp. nov. (Copepoda: Tisbidae) parasitic on a hydrothermal vent octopod and a reinterpretation of the life cycle of cholidyinin harpacticoids. *Cahiers de Biologie Marine* 41, 241–253.
- Matabos M., Thiébaud E., Le Guen D., Sadosky F., Jollivet D. and Bonhomme F.** (2008) Geographic clines and stepping-stone patterns detected along the East Pacific Rise in the vetigastropod *Lepetodrilus elevatus* reflect species crypticism. *Marine Biology* 153, 545–563.
- McDowall R.M.** (2008) Jordan's and other ecogeographical rules, and the vertebral number in fishes. *Journal of Biogeography* 35, 501–508.
- Muus B.** (2002) The *Bathypolypus*–*Benthooctopus* problem of the North Atlantic (Octopodidae, Cephalopoda). *Malacologia* 44, 175–222.
- Norman M.D.** (1992) *Amelooctopus litoralis*, gen. et sp. nov. (Cephalopoda: Octopodidae), a new shallow-water octopus from tropical Australian waters. *Invertebrate Taxonomy* 6, 567–582.
- Norman M.D., Hochberg F.G. and Boucher-Rodoni R.** (2005) A revision of the deep-water octopus genus *Scaeurgus* (Cephalopoda: Octopodidae) with description of three new species from the Southwest Pacific Ocean. *Journal of Molluscan Studies* 71, 319–337.
- O'Reilly K.M. and Horn M.H.** (2004) Phenotypic variation among populations of *Atherinops affinis* (Atherinopsidae) with insights from a geometric morphometric analysis. *Journal of Fish Biology* 64, 1117–1135.
- Roper C.F.E. and Voss G.L.** (1983) Guidelines for taxonomic descriptions of cephalopod species. *Memoirs of the National Museum of Victoria* 44, 49–63.
- Strugnell J., Voight J.R., Collins P.C. and Allcock A.L.** (2009) Molecular phylogenetic analysis of a known and a new hydrothermal vent octopod: their relationships with the genus *Benthooctopus* (Cephalopoda: Octopodidae). *Zootaxa* 2096, 442–459.
- Tåning Å.V.** (1952) Experimental study of meristic characters in fishes. *Biological Review* 271, 169–193.
- Toll R.B.** (1988) The use of arm sucker number in octopodid systematics (Cephalopoda: Octopoda). *American Malacological Bulletin* 6, 207–211.
- Voight J.R.** (1991) Morphological variation in octopod specimens: reassessing the assumption of preservation-induced deformation. *Malacologia* 33, 241–253.
- Voight J.R.** (2001) Morphological deformation in preserved specimens of the deep-sea octopus *Graneledone*. *Journal of Molluscan Studies* 67, 95–102.
- Voight J.R.** (2005) Hydrothermal vent octopus, *Vulcanoctopus hydrothermalis*, feeds on bathypelagic amphipods of *Halice*. *Journal of the Marine Biological Association of the United Kingdom* 85, 985–988.
- Voight J.R., Zierenberg R.A., McClain J., Batson P., Beers K., Daly M., Dushman B., Gollner S., Govenar B., Haney T.A., Hourdez S., Liow L.H., Parker C., Von Damm K., Zekely J. and Zelnio K.A.** (2004) FIELD Cruise to the Northern EPR: discoveries made during biological investigations from 8°37'N to 12°48'N. *RIDGE 2000 Events* 2, 22–24.
- Voss G.L. and Percy W.G.** (1990) Deep-water octopods (Mollusca; Cephalopoda) of the Northeastern Pacific. *Proceedings of the California Academy of Sciences* 47, 47–94.
- Won Y., Young C.R., Lutz R.A. and Vrijenhoek R.C.** (2003) Dispersal barriers and isolation among deep-sea mussel populations (Mytilidae: *Bathymodiulus*) from eastern Pacific hydrothermal vents. *Molecular Ecology* 12, 169–184.
- and
- Young R.E. and Mangold K.M.** (2000) *Tree of Life cephalopod Pseudomorph Function*. [http://tolweb.org/accessory/Cephalopod\\_Pseudomorph\\_Function?acc\\_id=1964](http://tolweb.org/accessory/Cephalopod_Pseudomorph_Function?acc_id=1964)

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