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Distinguishing between the abyssal macrourids *Coryphaenoides yaquinae* and *C. armatus* from *in situ* photography

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ABSTRACT

The scavenging fish communities at abyssal depths of the Pacific Ocean are dominated by two species of macrourids; the rough abyssal grenadier *Coryphaenoides yaquinae* Iwamoto and Stein, 1974 and the abyssal grenadier *C. armatus* (Hector, 1875). These two species are morphologically very similar, and in the absence of physical specimens are notoriously difficult to distinguish from photographic data. In an era of increasing reliance on imaging technology in the deep sea, we provide an analysis of images of the two species from around the Pacific Rim with supplementary data from the Atlantic and Southern Oceans. Our results show that image-specific morphometric characters are inadequate to distinguish the two species. However, the way in which artificial illumination is reflected from the body is both sufficient, and consistently different to distinguish between the two species. The results are also corroborated by known geographic and bathymetric distributions. This analysis is intended to provide a reliable method of identification from deep-sea imaging systems in the absence of standard fishing techniques.

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1. Introduction

The scavenging fish community at abyssal depths of the world oceans are dominated by the macrourids (or grenadiers). The abyssal plains of the Pacific Ocean are dominated by the rough abyssal grenadier *Coryphaenoides yaquinae* Iwamoto and Stein, 1974. The cosmopolitan abyssal grenadier *Coryphaenoides armatus* (Hector, 1875) is ubiquitous across the Atlantic, Southern and Indian oceans, and the deep continental slopes and rises of the Pacific Rim. Both species are readily attracted to bait, often in large numbers, which has resulted in these two species being the subject of both numerous and diverse scientific investigations for decades (*e.g.* Smith, 1978; Armstrong et al., 1991, 1992; Priede and Smith, 1986; Smith et al., 1992; Collins et al., 1999; Bailey et al., 2002; Drazen, 2002; Barry and Drazen, 2007; King and Priede, 2008, Yeh and Drazen, 2011).

Upon reviewing the two species, Wilson and Waples (1983) concluded that *C. armatus* is a wide-ranging, mostly eutrophic, deep-slope/upper-rise species which dominates the abyssal regions of the Atlantic and Indian Oceans between 2000 and 4800 m. However, in the Pacific Ocean, it is restricted to relatively food-rich environments between 2000 and 4300 m, unable to penetrate into the large oligotrophic expanses of the abyssal

plains. In the Pacific Ocean, the closely related congener, *C. yaquinae*, dominates abyssal depths as a result of metabolic adaptations for life in a comparatively oligotrophic region, free of competition, yet is absent in the North Atlantic despite similar depth, low temperatures and oligotrophic setting. *Coryphaenoides yaquinae* is confined to the Pacific, where it dominates under the vast expanse of the central gyres and is known to inhabit a depth range of 3400 to 5800 m (Wilson and Waples, 1983). Therefore, there is a small depth range of 900 m (3400–4300 m) where the two species co-exist on the Pacific continental slopes but are generally bathymetrically segregated (Endo and Okamura, 1992). The role of *C. yaquinae* as the deeper of the two species is evident in more recent samples reported from 6380–6450 m (Endo and Okamura, 1992) as well as photographic and video observations from 6160 m and 6945 m (Horibe, 1982; Jamieson et al., 2009c, respectively).

These two species are notorious for being almost indistinguishable from one another based on external morphology as reported by Wilson and Waples (1983, 1984) who highlighted erroneous identification by others such as Pearcy et al. (1982), Stein and Pearcy (1982); Smith et al. (1979). *Coryphaenoides yaquinae* and *C. armatus* are very closely related and easily confused and, for a period, thought to be the same species (Iwamoto and Stein, 1974). In the presence of physical and comparative specimens, *C. yaquinae* and *C. armatus* can be distinguished by differences in the number and arrangement of premaxillary and mandibular rows of teeth, or by DNA barcoding.

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In addition, the two species differ in the mean number of ventral fin rays, mean number of first dorsal soft rays and in the ranks of values of orbital length/head length (Wilson and Waples, 1983). Iwamoto and Stein (1974) also noted differences between C. armatus and C. yaquinae in squamation and coloration. They reported differences in scale morphology and the degree of scale-less area on the anterolateral regions of the snout. However, Wilson and Waples (1983) reported wide variation in squamation features, and rather showed electrophoretic differences between the two species. However, all these methods rely on obtaining physical specimens for examination.

In an age where scientific endeavour is pushing more regularly into deeper waters, there is a heavier reliance on still photography and video. When undertaking biological surveys in the hadal trenches (6500–11,000 m deep), this reliance is exacerbated in that most research vessels do not carry sufficient wires to tow bottom trawls or epibenthic sledges. In the absence of wire deployed sampling, free-falling lander vehicles equipped with baited cameras and/or traps have been regularly used in research campaigns as an alternative to net sampling (Jones et al., 2003; Bailey et al., 2007; Yeh and Drazen, 2009, 2011; Jamieson et al., 2011). One such campaign, the HADEEP project (2006–2011; Jamieson et al., 2009a), obtained video footage and still images of bait-attending fish from the Japan, Kermadec and Peru-Chile trenches with additional data from the Mariana abyssal plains (Jamieson et al., 2009c, 2011; Fujii et al., 2010). One of the components to these studies was the investigation into the geographic and bathymetric distribution of hadal fishes. In order to examine these patterns (as well as those of other taxa), comparative sampling was required to take place on the surrounding abyssal plains to either prove or refute hadal or trench endemism, and to determine the lower bathymetric limits of fish species. In the trenches, the fishes present were primarily found to be liparids inhabiting depths of 6900–7700 m (Fujii et al., 2010).

On the abyssal plains that surround the hadal trenches, the bait-attending fish communities are comprised of both Coryphaenoides yaquinae and C. armatus. Whilst these species can be readily distinguished by either genetics or certain morphological characters, such determinants of species are not measureable in photographic images. Baited cameras, and other methods of in situ imaging (e.g. Bailey et al., 2006), are disadvantaged in their inability to determine accurate species identification, particularly between co-inhabiting, similar species such as C. yaquinae and C. armatus.

On reviewing images from within the data archives of the HADEEP project and other work undertaken by the University of Aberdeen, it became apparent that a distinction could be made between the Coryphaenoides spp. inhabiting similar depths or co-inhabiting the same depth. This distinction was based on the manner in which artificial light is reflected off the surface of the body. The distribution of these photographic data amongst various scientists specialising in deep-sea fish led to two interesting opinions; (1) that the macrourids with the lighter, more reflective and seemingly more robust appearance was C. armatus whilst the darker, more gnarled textured species was C. yaquinae, although these conclusions were derived on 'hunches' based on personal experience. (2) Some experts believed that the shade or colour, and to some degree, the texture of the fish was simply an artefact of the distance of the fish to the landers lights, i.e. the paler, more reflective fish were closer to the flash and the darker ones were further away. Although hitherto anecdotal, there are now sufficient data to examine these occurrences in a more analytical manner.

This study is based on collated image data from around the Pacific Rim with comparative Southern and Atlantic ocean data, to examine how to distinguish C. yaquinae from C. armatus in instances of co-inhabitation. The approach was to examine; (1) Whether image-specific morphological measurements could be made to determine species identification, (2) Whether the physical appearance is sufficient to distinguish the two species, (3) whether the artificial illumination from the lander vehicle alters the appearance of fish at certain distances and (4) whether the results could be corroborated by the known bathymetric and geographic distribution of the species.

2. Materials and methods

All still photography taken in the Pacific Ocean was to obtained using Hadal-lander B (Jamieson et al., 2009a) with one supplemental video from Hadal-Lander A in the Japan Trench (Jamieson et al., 2009bc). Hadal-lander B was a free-falling lander equipped with a 5 megapixel digital still camera (OE14-208; Kongsberg Maritime, UK). Illumination was provided by a single flashgun (OE11-242; Kongsberg Maritime, UK) which has a light output of 80 W maximum and a beam angle of 55°. On the Hadal-lander, the flash output is set to $^3/_4$, (60 W). The camera was mounted vertically at an altitude 1 m above the seafloor providing a visible area of 62×46.5 cm (0.29 m^{-2}). In the centre of the field-of-view was a parcel of bait (~ 1 kg of tuna or mackerel). A 1 cm diameter scale bar was also in the centre of the field of view, positioned to intersect the sediment-water interface upon landing. Time-lapse images were taken at 60 s intervals. The Hadal-Lander A had a 3CCD colour video camera arranged in the same way as Hadal-Lander B and programmed to take 1 min of footage every 5 min. Illumination was provided by two 50 W halogen bulbs also positioned at 1 m above bottom. To permit comparison with Atlantic and Southern Ocean data, images from the ROBIO lander were used (Jamieson and Bagley, 2005). The ROBIO and Hadal-Landers use the same camera and flash system and differ only in camera altitude above bottom; Hadal-Lander=1 m above bottom, ROBIO=2 m above bottom.

The landers descended to the seafloor by virtue of negatively buoyant ballast weights. At the end of the experimental period the ballast was jettisoned by acoustic command from the surface. All images were obtained autonomously and upon retrieval, all imaging data were downloaded.

A list of deployments and additional details where abyssal macrourids were observed are listed in Table 1, and comprise three trench locations (Japan, Kermadec and Peru-Chile Trench), and three abyssal plain locations; the Mariana Abyssal Plain in the central Pacific, the Crozet Plateau in the Southern Ocean and the Porcupine Abyssal Plain in the Northeast Atlantic Ocean (Fig. 1). The Southern and Atlantic Ocean data were used as control locations as comparative trawl data were available to confirm the observed species were C. armatus and that C. yaquinae is not present in either of these two locations (Priede et al., 2010; Cousins and Priede, submitted).

2.1. Morphometric data

The nature of photography is such that accurate measurements of standard morphological characteristics, such as head length, orbit diameter, pre-anal length, and counting features such as fin rays are not possible as a result of either visible obstruction or perspective. Therefore, to achieve comparative morphological determinants, alternative measurements had to be made from the photographic data. Of all the images, only the fish which were positioned horizontally relatively to the seafloor were used. To account for altitude and body size, actual measurements could not be determined with confidence, therefore

Table 1
Deployment details of image data from deployments where either *C. yaquinae*, *C. armatus*, or both were observed and used in this study.

Site	Image type [altitude; m]	Depth (m)	Latitude	Longitude	Ocean	Location	Date	Vessel
1	Stills [2]	4668	48°59'N	16°43'W	NE Atlantic	Porcupine Abyssal Plain	040811	*James Cook*
2	Stills [2]	4242	45°50'S	56°06'E	Southern	Crozet Plateau	211205	*Discovery*
3	Video [1]	6945	40° 15'	144° 30'E	NW Pacific	Japan Trench	301007	*Hakuho-Maru*
4	Stills [1]	5469	18° 49'N	149° 51'E	Central Pacific	Mariana Abyssal Plain	291107	*Kairei*
5	Stills [1]	4329	36° 45'S	179° 11'W	SW Pacific	Kermadec Trench	091109	*Kaharoa*
5	Stills [1]	5172	36° 30' S	179° 12'W	SW Pacific	Kermadec Trench	051109	*Kaharoa*
5*	Video [1]	5173	36° 31' S	179° 12'W	SW Pacific	Kermadec Trench	051109	*Kaharoa*
5*	Stills [1]	6000	36° 10' S	179° 00'W	SW Pacific	Kermadec Trench	071109	*Kaharoa*
6	Stills [1]	4602	06° 12'S	81° 40'W	SE Pacific	Peru-Chile Trench	030910	*Sonne*
6*	Stills [1]	5329	04° 27'S	81° 54'W	SE Pacific	Peru-Chile Trench	010910	*Sonne*

* Indicates deployments where fish were visible but, as a result of very low numbers and orientations of un-measureable characters, were not included in the morphometric analyses.
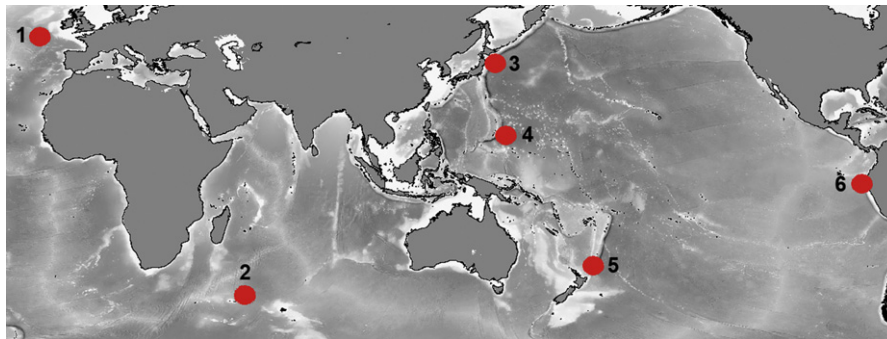

Fig. 1. Map of study sites where 1=Porcupine Abyssal Plain (4668 m; NE Atlantic), 2=Crozet Plateau (4242 m; Southern Ocean), 3=Japan Trench (6945 m; NW Pacific Ocean), 4=Mariana Abyssal Plain (5469 m; Central Pacific Ocean), 5=Kermadec Trench (4329 m, 5172 m; SW Pacific Ocean), 6=Peru-Chile Trench (4602 m; SE Pacific Ocean).

multiple measurements were made and converted to relative ratios. The measurements taken were therefore all theoretically projected on a 2-dimensional plane; interorbital (IO), head length (HL), head width (HW) and snout to dorsal length (SD) as defined in Fig. 2. These measurements were taken using the proprietary image analysis software (ImageJ; NIH, USA). The measurements were converted to relative ratios by dividing HL by IO (HL:IO), HL by HW (HL:HW), SD by HW (SD:HW), and SD by HL (SD:HL). To avoid measuring the same fish twice, a selection of images were used every 30 minutes into each deployment, whilst only selecting fish in a horizontal position. Total length (TL) was not measured because at a 1 m altitude, most individuals are not observed in their entirety and TL is also not a distinguishing characteristic of the two species.

One way analyses of variance (ANOVA) were used to compare the mean morphometric ratios (HL:IO, HL:HW, SD:HW and SD:HL) between the sampling locations. Areas compared were the Atlantic Ocean ($n=29$), Southern Ocean ($n=21$), Kermadec Trench ($n=35$), Peru-Chile Trench ($n=28$) and the Marianas Trench ($n=13$). The Japan Trench was excluded from the analysis due to insufficient data ($n=1$). Fligner-Killeen tests were used to confirm homogeneity of variance. When significant differences were obtained from one way ANOVAs, Tukey's Honestly Significant Different (HSD) test was applied for pair-wise comparisons of areas. Morphometric-ratios of light and dark individuals from the Kermadec ($n=24$ and 11, respectively) and Peru-Chile Trench ($n=24$ and 4, respectively) locations were compared using Student's t-tests.

2.2. Effects of illumination and visual comparisons

To examine the effects of artificial illumination on the appearance of fish at varying proximity to light, three techniques were used. (1) on the baited camera deployments from the Atlantic and
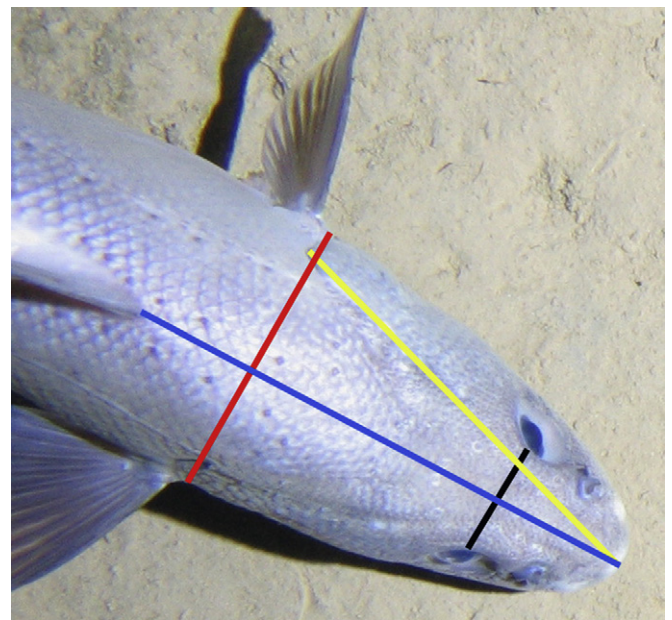
Fig. 2. Morphometric measurements used from photographic data where the black line=inter-orbital length (IO), the yellow line=Head length (snout to gill; HL), the red line=head width (HW) and the blue line=snout to dorsal fin (SD). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Southern oceans, where the camera altitude was 2 m, images containing multiple individuals of the same known species (*C. armatus*) at different altitudes above bottom (and therefore proximity to the lights) were selected and manually assessed. (2) In the case of the Kermadec Trench location, where light

individuals were observed at 4329 m and dark individuals at 5172 and 6000 m, images were selected which contained fish of both appearances in similar positions and proximity relative to the light, and of similar body size. These selected images were collaged and manually assessed. (3) In the case of the Peru-Chile Trench location, where both light and dark individuals were observed simultaneously, select images were identified and manually assessed where different combinations of concurrent light and dark fish were present at equal proximity to the flash.

To assess the similarity in appearance between locations, images were selected from each site at each depth whereby individual fish were in a similar position and proximity to the light, and of a similar body size. In the case of the Atlantic and Southern Ocean data, only fish that were approximately one metre above the seafloor, thus one metre from the light, were used to provide direct comparisons with the Pacific data. These images were manually collaged and assessed.

3. Results

3.1. Morphometric data

One way ANOVAS showed significant differences in morphometric ratios between all the locations sampled (Table 2), including significant differences between the Atlantic and Southern ocean sites where both species are known to be *C. armatus* (Priede et al., 2010; Cousins and Priede, submitted). No significant differences were found between mean morphometric ratios of light and dark individuals indentified in the Kermadec and Peru-Chile Trench locations (Table 2; Fig. 3).

3.2. Effects of illumination and visual comparisons

The selected images from the Kermadec Trench location show that at equivalent positions and proximity to the light, the fish were consistently dark-grey in appearance at 5173 m and extremely light at 4329 m. In the Peru-Chile Trench location, where both light and dark individuals were observed simultaneously, there were multiple images showing both at equal proximity to the light. These included images showing light and dark individuals in alternate positions, confirming that proximity to the light does not account for the differences in appearance (Fig. 4ab). The selected images from the Southern and Atlantic locations consistently showed that *C. armatus* appears dark grey at a distance of 2 m. However, on many occasions, individuals were observed ascending (or descending) from (or towards) the seafloor, and when within approximately 1 m from the light they appeared pale and white (Fig. 4cd). It is also worth noting that the Southern Ocean *C. armatus* are generally much paler in appearance than the Atlantic populations; however the lightening of the skin tone in close proximity to the light still occurs. This effect is also evident from other images from similar baited cameras (Yeh and Drazen, 2011). Video footage from the 6945 m deployment in the Japan Trench, where the species are known to be *C. yaquinae*, showed no apparent lightening of the skin tone in proximity to the light. Although there were only three individuals present throughout the deployment, there did not appear to be any lightening effect between a distance of 1 and 0.5 m to the 50 W halogen bulb.

By collating corresponding images of the light and dark species from each location it appeared extremely convincing that the lighter species are indeed *C. armatus* and that the darker species is *C. yaquinae* (see Figs. 5 and 6, respectively). The lightening of *C. armatus* results in almost all fine detail on the snout, head and dorsal surface being lost whereas in *C. yaquinae*, despite being at equal distance to the flash, the surface texture of these areas are still clearly visible. In *C. armatus* the only clear features remaining during illumination are dark circles around the eyes and no lightening of the dorsal or pectoral fins were evident (Figs. 4ab, 5). There was also no evidence of a spectrum between light and dark individuals in either the Peru-Chile or Kermadec Trench images, thus discounting variation within one population.

Table 2
Results of ANOVA tests investigating differences in morphometric ratios between areas of the Atlantic Ocean, Southern Ocean, Kermadec Trench, Peru-Chile Trench and the Marianas Trench. P-values derived from Tukey's Honestly Significant Different (HSD) multiple area comparisons. Results of Student's t tests investigating differences in mean morphometric ratios between light and dark individuals observed in the Kermadec and Peru-Chile Trenches.

	Head length: Inter orbital	Head length: Head width	Snout dorsal: Head width	Snout dorsal: Head length
ANOVA				
F	22.217	27.541	15.405	14.711
DF	4	4	4	4
p-value	< 0.001	< 0.001	< 0.001	< 0.001
Tukey's HSD				
Atlantic—Kermadec	< 0.001	0.946	< 0.001	< 0.001
Atlantic—Marianas	< 0.001	0.001	0.093	< 0.001
Atlantic—Peru-Chile	< 0.001	< 0.001	< 0.001	0.001
Atlantic—Southern	0.027	0.008	0.985	0.136
Kermadec—Marianas	0.365	< 0.001	0.962	0.038
Kermadec—Peru-Chile	0.146	< 0.001	0.098	0.817
Kermadec—Southern	0.061	< 0.001	< 0.001	0.086
Marianas—Peru-Chile	1.000	< 0.001	0.089	0.004
Marianas—Southern	0.002	0.843	0.045	< 0.001
Southern—Peru-Chile	< 0.001	< 0.001	< 0.001	0.570
Student's t-test (Kermadec)				
T	1.113	1.662	−0.118	−1.535
DF	33	33	33	33
p-value	0.274	0.106	0.907	0.134
Student's t-test (Peru-Chile)				
T	−0.329	−0.003	−0.131	−0.287
DF	26	26	26	26
p-value	0.745	0.997	0.897	0.776
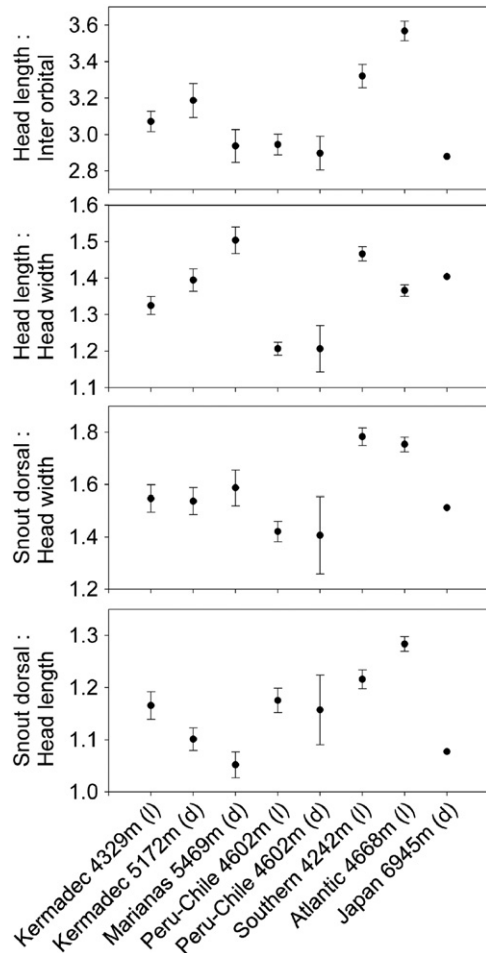
Fig. 3. Mean (± standard error) morphometric ratios from images of light (l) and dark (d) individuals in the Kermadec, Marianas, Peru-Chile and Japan Trenches and the Southern and Atlantic Oceans.

4. Discussion

These comparative image data provide both corroborative data on the distribution of *C. yaquinae* and *C. armatus* and provide methodology for distinguishing the two species from baited cameras. It is quite clear that using image-specific morphological characters to distinguish the two species is highly variable and insufficient, especially given that significant differences were found between the two locations where the species are known to be *C. armatus*, and were of similar body size. Also, variation in morphology between *C. armatus* populations in the Atlantic and Pacific Oceans are known (Iwamoto and Stein, 1974; Wilson and Waples, 1983, 1984). The data reported here may simply indicate that the differences between two species are so slight they are masked by the variation within *C. armatus* and/or different *C. armatus* populations. Alternatively, the differences between the two species may be so slight they are masked by the measurement error associated with using images as opposed to measuring physical specimens. Furthermore, Wilson and Waples (1984) indentified a distinct subspecies of *C. armatus* in the NE Pacific based on electrophoretic and biometric (morphometric+meristic) variation; *Coryphaenoides armatus variabilis*, distinct from the others; *Coryphaenoides armatus armatus*. Whilst this study does not include any data from the slopes of the NE Pacific, it is highly unlikely these two subspecies could be distinguished from *in situ* photography, but does however reiterate subtle variation within the species.
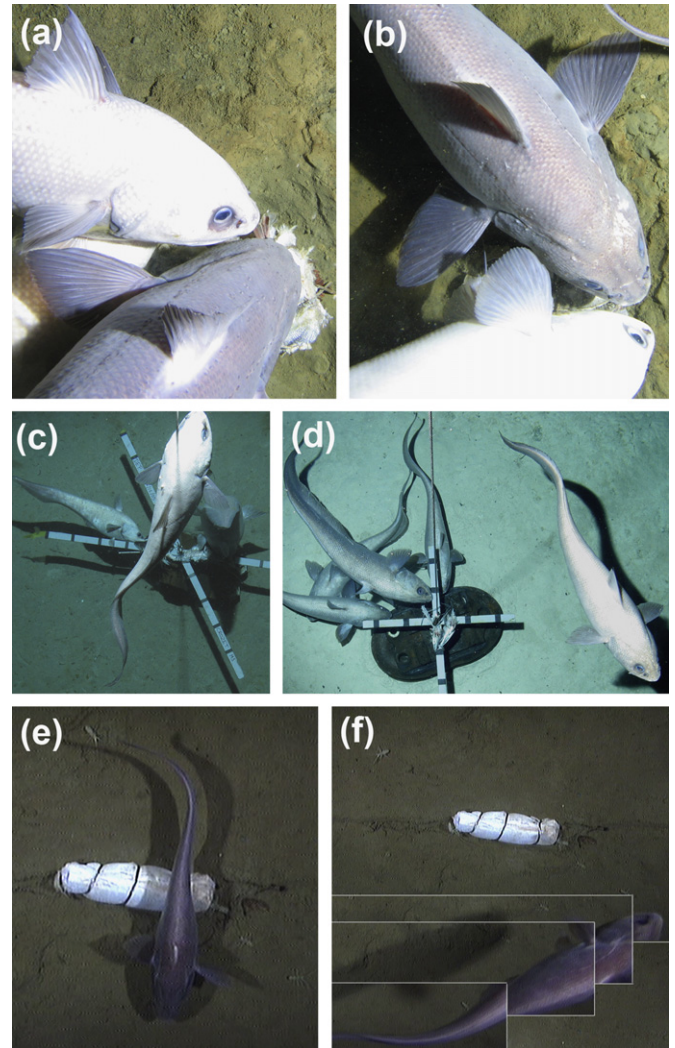

Fig. 4. Effects of proximity to artificial illumination do not account for differences in appearance. Image (a) shows both light and dark individuals at equal distance from the light and (b) in alternative positions at equal distance to the light, revealing distinctive differences in appearance (a and b are from the Peru-Chile Trench). The flash is pointing from the above right hand side (see shadows). Images from the Southern (c) and Atlantic (d) location show in the background, at 2 m from the light, *C. armatus* appear dark, whereas in the foreground, at approximately 1 m from the light, they appear much paler. Images (e) and (f) from 6945 m in the Japan Trench show that *C. yaquinae* does not significantly lighten from a distance of 1 m (e) to 0.5 m (f). Image (f) is a whole fish reconstruction from video footage, each frame indicated by grey box.

Using the reflectance and general appearance of this fish appears to provide an adequate means of distinguishing the two *Coryphaenoides* species. Reflectance of light or silvery appearance in the skin of fishes is generally attributed to the presence of guanine crystals in the integument (Denton and Land, 1971). This raises the question as to whether the difference in appearance of *C.yaquinae* and *C. armatus* in images is the result of differences in concentration of guanine in the epithelium or differences in arrangement of the reflectors. Reflectors in fishes often consist of multilayer stacks of alternating high and low refractive index materials, *e.g.* guanine crystals and cytoplasm, respectively, The colour of this reflection changes with viewing angle, whereby the more oblique the viewing angle, the shorter the wavelength (towards the blue end of the spectrum). Such reflectors can be highly wavelength selective enabling iridescent colorations, but some species achieve white light reflectance through randomised arrangement of reflector elements (MacKenzie at al., 1995).
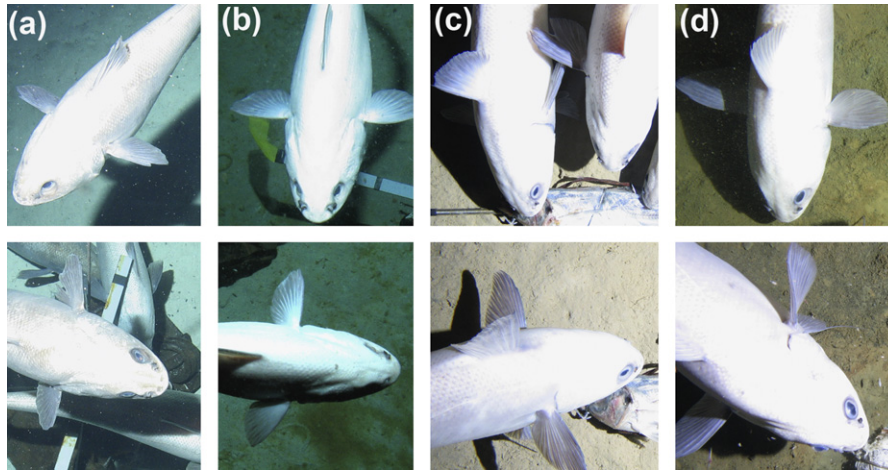
Fig. 5. Comparative images of *Coryphaenoides armatus*. Images (a) and (b) are from the NE Atlantic and Southern Ocean respectively, (c) is from the Kermadec Trench and (d) the Peru-Chile Trench. The Atlantic and Southern Ocean images, known to be *C. armatus*, are of individuals at equal distance to the camera than in the other images (1 m from the camera and flash).
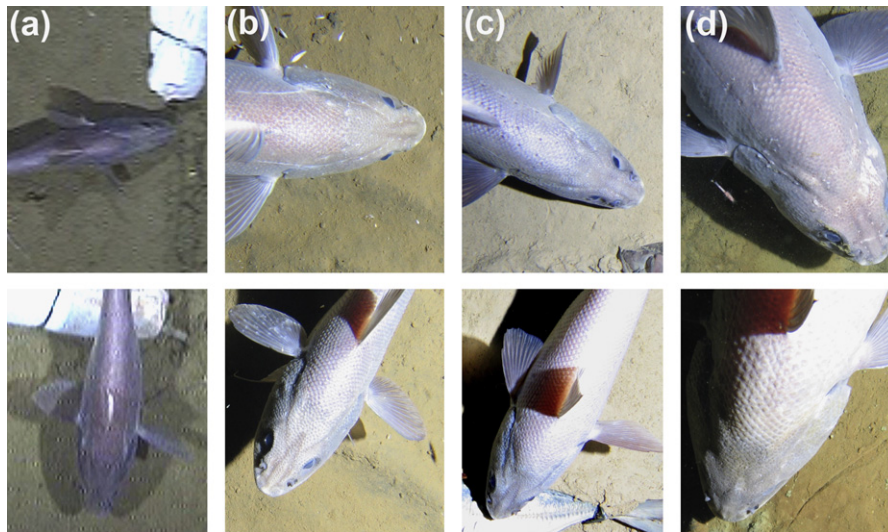
Fig. 6. Comparative images of *Coryphaenoides yaquinae*. Image (a) is from the Japan Trench, (b) the Mariana Abyssal Plain, (c) the Kermadec Trench and (d) the Peru-Chile Trench. All images were taken from 1 m above bottom. With the exception of the Japan Trench images, the fish are all in the same position relative to the flash and camera.

Although neither of these two species can be considered a silvery fish, they do require large quantities of guanine crystals in the swim bladder wall to confer gas impermeability at high pressure (Ross and Gordon, 1978). In eels there is an association between silveriness in the skin and increase in guanine in the swim bladder during adaptation to deepwater oceanic migration (Kleckner, 1980).

Differences in roughness may also affect the way light is reflected from the body of each of the species. The scales of *C. yaquinae* have been described as notably coarser and the spinule ridges more erect and fewer than those found in comparable sized *C. armatus* (Iwamoto and Stein, 1974; Wilson and Waples, 1984). A rough surface scatters light to a greater degree than a smooth surface, resulting in a more diffuse reflection of light (Stover, 2005). The relatively smooth surface of *C. armatus* may reflect more light towards the camera, resulting in a lighter appearance. Iwamoto and Stein (1974) also noted slight differences in coloration between the two species, but these were, however, not readily apparent unless specimens of both species were compared directly. Interestingly, they noted the opposite to that viewed by the camera in this study in that *C. yaquinae* appear lighter with a grayish cast, whereas *C. armatus* were a darker brownish black (contrary to the images shown in Endo and Okamura, 1992 and this study). The coloration incongruence between *in situ* and laboratory comparisons may well have contributed to the reluctance to identify to species level from *in situ* photography (*e.g.* Bailey et al., 2006). These observations do however highlight distinct differences in squamation and coloration between the two species. The results presented here add to these by highlighting that the differences in reflected light from the body is consistent and sufficient to distinguish between the two species from *in situ* photography.

The accuracy of these distinctions is also corroborated by the known bathymetric and geographic distribution of both species. Whilst there are no deployments at depths < 6945m in the Japan Trench, the data presented here, also shown in Jamieson et al. (2009c) are in good agreement with Iwamoto and Stein (1974), Horibe (1982) and Endo and Okamura (1992), that the abyssal grenadier in this region at these depths are *C. yaquinae*. However, there are records of co-inhabitation with *C. armatus* in this area on the continental slopes at 4100-4220 m (Endo and Okamura, 1992) which again is in agreement with the Kermadec and Peru-Chile Trench data reported here and other studies from the NE Pacific (Yeh and Drazen, 2011).

Table 3
Percentage occurrence of *C. yaquinae* and *C. armatus* at the Pacific Ocean locations, ordered by depth and based on number of observations including number of frames and percentage of frames present. For direct comparison, all data were taken from the first 12 hours into the deployment.

Location	Depth (m)	% *C. armatus*	% *C. yaquinae*	Number of observations in [number of frames]	%frames
Kermadec	4329	100	0	252 [190]	26.4
Peru-Chile	4602	95	5	277 [199]	27.6
Kermadec	5172	0	100	59 [57]	7.9
Peru-Chile	5329	0	100	16 [16]	2.2
Mariana	5469	0	100	162 [139]	19.3
Kermadec	6000	0	100	2 [2]	0.3
Japan	6945	0	100	3 [3]	2.4*

* Indicates % presence in 1 min video sequences every 5 min over 10.5 hours.

This study also suggests that the grenadiers observed on the Marianas Abyssal Plain were exclusively *C. yaquinae*, which is in agreement bathymetrically, and perhaps in the absence of any major continental slopes or rises, confirms the explanation for the absence of *C. armatus* as suggested by Wilson and Waples (1984), albeit the depth is perhaps too great. Other studies in the Central Pacific, some distance from major continental slopes, also reported the presence of *C. yaquinae* (at 4753 m) but not *C. armatus* despite covering a depth range of 4500 m (Yeh and Drazen, 2009). However, using the same baited camera technique down the adjacent NE Pacific slopes, they observed *C. armatus* at 3000 m (Yeh and Drazen, 2011). Confirmation of *C. yaquinae* in the northwest and central Pacific at depths exceeding ~5000 m supports our analysis of the comparative visual dataset which indicates that the deeper, darker, species of the Kermadec and Peru-Chile trenches are *C. yaquinae*. Likewise the similarity in appearance and bathymetric ranges of the lighter species of the two South Pacific locations compared to the Southern and Atlantic Ocean images provides compelling evidence to suggest that at depth < 5000 m, the species are *C. armatus*. The slopes off New Zealand, near the Kermadec Trench location, are also the type locality of *C. armatus* (Hector, 1875). It is interesting to point out distinct trends between the two species in the Kermadec region, where all individuals at 4329m were *C. armatus* and all those observed at 5173 m were *C. yaquinae*, and the only deployment where the two were seen simultaneously was at 4600 m in the Peru-Chile trench (Table 3). Although this is potentially an artefact of limited bathymetric sampling resolution, it does insinuate a potentially very acute bathymetric segregation between the two species, as also mentioned by Endo and Okamura (1992).

It is also worth noting that in the Kermadec Trench other deployments were carried out at 6007, 6890, 7199, 7561 and 7966 m and no macrourids were observed. Likewise, in the Peru-Chile Trench deployments at 6173, 7050 and 8074 m revealed no presence of macrourids, and in the Japan Trench at 7703 m no further observation of macrourids were obtained. Other deep deployments have been made in the Izu-Ogasawara Trench (NW Pacific) and Tonga Trench (SW Pacific) at depths exceeding 8100m and no fish were found. All fish found deeper than the 6945 m record of *C. yaquinae* in the Japan Trench were liparids between 6945 and 7703 m (Fujii et al., 2010). There is therefore a convincing likelihood that macrourids, in particular *C. yaquinae*, are limited to the abyssal plains, and on occasion the upper depths of the trenches (the abyssal-hadal transition zone).

5. Conclusion

These data show that despite baited cameras inhibiting the conventional taxonomic measurements required to confirm

identification, in areas were two species as ubiquitous as *C. yaquinae* and *C. armatus* co-inhabit, there are means by which to distinguish the two. Using the illumination from the camera system to differentiate the two species is a technique discovered following anecdotal comments regarding the general appearance by taxonomists and not distinct morphological characters *per se*. However, the significance was perhaps not realised as conventional taxonomy does not occur in such settings. These findings are important in preventing misidentifications such as those by Wilson and Waples (1984), and more recent reports whereby the original description of the Kermadec Trench fish fauna by Jamieson et al. (2011) have, in light of this study, misidentified *C. armatus* individuals at 4329 m as *C. yaquinae*. Furthermore, as *in situ* photography in the deep-sea is used more frequently, these sorts of data, however species specific, are extremely valuable in reliably interpreting faunal communities.

These studies are not intended to promote imaging vehicles as an alternative to conventional taxonomy, as there is no substitute for the collection of physical specimens. However, it is intended to provide the means by which to aid identification when using such systems in the absence of standard fishing techniques.

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