Deep-reef fish assemblages of the Great Barrier Reef shelf-break (Australia)

Tiffany L. Sih1,2, Mike Cappo3 & Michael Kingsford1

Tropical mesophotic and sub-mesophotic fish ecology is poorly understood despite increasing vulnerability of deeper fish assemblages. Worldwide there is greater fishing pressure on continental shelf-breaks and the effects of disturbances on deeper fish species have not yet been assessed. Difficult to access, deeper reefs host undocumented fish diversity and abundance. Baited Remote Underwater Video Stations (BRUVS) with lights were used to sample deeper habitats (54–260 m), in the Great Barrier Reef (GBR), Australia. Here we describe fish biodiversity, relative abundance and richness, assessing the prediction that depth would drive assemblage structure in the GBR. Distinct groups of fishes were found with depth whilst overall richness and abundance decreased steeply between 100 and 260 m. Commercially-valuable Lutjanidae species from Pristipomoides and Etelis genera, were absent from shallower depths. Few fish species overlapped between adjacent depth strata, indicating unique assemblages with depth. We also detected new location records and potential new species records. The high biodiversity of fish found in shelf-break environments is poorly appreciated and depth is a strong predictor of assemblage composition. This may pose a challenge for managers of commercial fisheries as distinct depth ranges of taxa may translate to more readily targeted habitats, and therefore, an inherent vulnerability to exploitation.

Fishes occupying deeper shelf-break environments are susceptible to increasing threats as the condition of many shallower coral reefs is in decline due to the effects of anthropogenic and environmental disturbances (e.g. fishing, pollution, coral bleaching and warming temperatures1–3). Deeper mesophotic reefs are extensions of shallow habitats and can play a critical role in maintaining the health of the greater ecosystem4. Deeper environments may be refuges for shallow-reef fishes threatened by fishing pressure4,5 and warming temperatures6. Worldwide, fishers are fishing deeper and more efficiently with better technology and gear7–9. The value of these ecosystems must be evaluated in the face of potential rapid future exploitation. What are critical – or irreplaceable – components to protect for future resources? Only by pushing the depth boundaries of ecological studies can we understand if deeper benthic habitats have similar or different patterns and processes. Further, to what degree are shallow and deep habitats connected? We need methods that can be used in both shallower and deeper habitats for comparisons over a broad geographic range.

There is a paucity of ecological information on the distribution and abundance of deep-reef fishes worldwide10,11. The light-limited depths of the mesophotic and sub-mesophotic, which traditionally has remained a mystery due to the greater logistics12 and costs11,13 of sampling deeper, and often remote, habitats. Mesophotic coral reefs can extend to 150 m in clear waters14,15 and this depth is thought to be the lower distribution of many reef-based species10,14–18, including fishes. Studies on mesophotic fish ecology may not sample the greater taxonomic diversity available15,18 because time, cost and expertise are often limited. Deep-reefs may have a disproportionally high number of novel or endemic species19–22. The current information on deeper fish distribution is also not evenly distributed worldwide; it is currently unclear whether deep-reef fishes are found in broad geographic ranges but so far are only found in a few explored locations21–23,29.

The greatest proportion of reef fish biodiversity studies are limited to depths shallower than 30 m10,22. This presents a large bathymetric gradient of reef communities that have not been explicitly described. Mesophotic fish and coral assemblages may change along depth gradients3,14,22 and may include shallower-occurring species,
but also deep-specialist species restricted to certain depths\(^1\). The Great Barrier Reef (GBR) comprises 2,500 reefs and represents the world’s largest continuous coral reef ecosystem covering approximately 344,400 km\(^2\). With over 1,500 known fish species in the Great Barrier Reef Marine Park (GBRMP), few studies include the mesophotic depths along the edge of the continental shelf. This shelf-break may potentially have greater species diversity than mesophotic reefs in other study locations\(^2\) as follows: (1) the western Pacific and Australia is close to the “centre of reef biodiversity”\(^3\), (2) the broad shelf of the GBR harbours greater diversity\(^4\) and (3) the amount of deeper reef habitat may have been previously underestimated\(^5\). The continental shelf-edge can be among the steepest of environmental gradients, subject to a wide range of environmental drivers that can significantly change over tens of meters and affect the faunal diversity (e.g. light availability, temperature, benthic substrate, and food availability)\(^6\) and we predicted that there would be distinct fish communities along this gradient.

Depth is likely a key driver of assemblage structure\(^7\),\(^8\),\(^9\),\(^10\) and evidence in the mesophotic so far concurs with this paradigm. Bathymetric breaks have been established for the GBR for coral species, including a transition at 60 m between distinct upper and lower mesophotic tropical assemblages\(^11\) and at subtropical latitudes around 50 m\(^12\). Fish species richness appears to increase to a maximum at 25–30 m, then decreases to 50–65 m\(^13\); however, these studies did not investigate deeper, to the maximum extent of these light-limited reef environments.

Understanding how species richness is distributed across environmental gradients, such as the shallow-to-deep reef transition zone, is key to understanding how species in both zones may respond to future environmental changes. Further, bathymetric distribution data can improve conservation and management efforts and reduce bycatch, by encouraging fisheries to target depth ranges with a high proportion of target species relative to unwanted species.

Monitoring techniques often focus on economically important fishes, limiting the ability to detect changes in whole fish assemblages\(^14\),\(^15\),\(^16\),\(^17\). Underwater video has great potential to document and monitor deep-reef communities of fish and can be constructed to survey deeper depths with adequate light. Specifically, Baited Remote Underwater Video Stations (BRUVS) have been used to monitor fish and benthic assemblages of the GBR, but not fish communities in deeper mesophotic and sub-mesophotic reef and inter-reefal habitats\(^18\),\(^19\). BRUVS are useful for studying deep-reef fishes, as they can withstand pressures associated with greater depths and are easily replicated for repeatable ecological studies (see reviews\(^20\),\(^21\),\(^22\)). Surveys with similar baited video equipment have assessed mesophotic fish communities in other locations, investigating abundance and size distributions\(^23\),\(^24\), habitat associations\(^25\),\(^26\), and the efficacy of Marine Protected Areas for fisheries management\(^27\). However, no studies have investigated below the 80 m isobath in the GBRMP\(^28\). BRUVS have inherent biases that have to be carefully considered, such as the presence of a bait plume, which can alter the behavior of fishes and preferentially attract larger, more mobile fishes (see reviews\(^29\),\(^30\),\(^31\)). However, an advantage of this method is that it is non-intrusive or destructive, thus BRUVS are permitted in most zones of the GBRMP. BRUVS are a good method in baseline and longterm deep-reef studies in the GBR as the images and video are geo-referenced and can be kept as a permanent record to validate fish identifications, or to compare species compositions over temporal and spatial scales with controlled sampling effort along a great depth range.

The objective of this study was to use BRUVS to investigate tropical fish assemblages in mesophotic to sub-mesophotic depths at a number of reefs along the shelf-edge of the central GBR (Fig. 1). We hypothesized that abundance of fishes and related diversity would vary with depth and that the patterns would be consistent by reef. This is the first comprehensive fishery-independent survey of mesophotic fish biodiversity within the GBR at depths of 50–300 m. Specifically, we aimed to: (a) determine how species richness and abundance vary with depth; (b) describe fish assemblages and identify key depth-indicator species; and (c) provide critical baseline information, which is archived for future comparisons; (d) measure thermal profiles of the water column, in multiple years where we hypothesized that temperature/depth strata may correlate with the distribution of fishes.

Seawater temperature varied greatly with depth (Fig. 2). At Myrmidon, CTD data from 2009–2013 indicated surface temperatures were about 25 °C and well-mixed to approximately 100 m. Temperatures dropped by up to 10 °C (i.e. 14–16 °C) from ~100 m to a depth of ~250 m. The thermocline commenced at 70–100 m and in many years a decrease in temperature continued to the 200–250 m depth stratum with some evidence that the rate of change slowed at the greatest depths we sampled. Although the steepness of the temperature change at the beginning and within the thermocline varied among years, the depth of the well-mixed shallow water layer was similar from year to year.

**Results**

A total of 1081 individual fish, sharks and rays were identified, representing 130 species from 29 families (48 BRUVS deployments, 42.35 hours of sampling-time). Species diversity varied with 1–40 species identified per deployment, average species richness was 9.44 species, and mean abundance of 22.5 fishes. Lutjanidae, Lethrinidae and Nemipteridae were the families most frequently sighted. The most speciose families were Labridae (23 spp), Carangidae (16 spp), Lutjanidae (16 spp), and Lethrinidae (11 spp). BRUVS allowed us to identify large-bodied fish such as groupers, jacks, snappers and apex predators such as sharks. Many commercially-valuable species were sighted including Pristipomoides filamentosus, Pristipomoides multidens, and Electrophorus electricus. Some smaller species and juveniles were only identified to genus (i.e. juvenile Lethinus sp.).

Some of the species seen at these depths are of conservation concern according to IUCN criteria\(^32\), these include: Scalloped Hammerhead and Humphead Maori Wrasse (Sphyraena lewini and Cheilinus undulatus, Endangered), Blotted Fantail Ray, Silvertip Shark and Sandbar Shark (Taeniura plumbea, Vulnerable), and Whitetip Reef Shark and Grey Reef Shark (Triaenodon obesus and Carcharhinus amblyrhynchos, Near Threatened).

Several of the species observations represent new geographic location records for Australia, and specifically the GBR (Table 1). These include: Chromis okamurae (143 m)\(^33\), Chromis miratoni (155–194 m)\(^34\), Chromis circumaurea (115 m)\(^35\) and the recently described Bodianus bennetti (155–179)\(^36,37\). Unrecognized species from
Selenanthias (143–160 m), Chromis (155 m), and Bodianus (143 m) were also observed and may potentially be new species (Supplementary video).

A number of small-bodied fishes were recorded and are likely an underestimate of true abundance and richness. Both Terelabrus rubriovittatus and Cirrhilabrus roseafascia appeared in a large proportion (17%) of the sites. Other frequently sighted smaller fish include small Bodianus species (25% of sites) and Pentapodus species (19%).

**Species richness and abundance with depth.** Strong depth-related patterns of relative species richness (number of species per 60 minutes of video) and total fish abundance (sum of MaxN of all species per deployment per 60 minutes of video) were detected and these differences were significant according to ANOVA (Table 2). There was no interaction between depth and site (@ p = 0.25) and therefore the interaction was pooled into the factor depth. Species richness and abundance generally decreased from shallow to deep although patterns varied by reef (Fig. 1). Comparing Shallow (50–115 m), Mid (128–160 m) and Deep (179–260 m) fish assemblage groups for species richness (t-tests), Shallow-Mid (p = 0.08, NS) and Mid-Deep (p = 0.06, NS) were not significantly different groups, but Shallow-Deep was (p = 0.02*). Tukey’s HSD highlighted the same differences in overall species richness between the depth groups: Shallow-Mid (p = 0.21, NS), Mid-Deep (p = 0.13, NS), and Shallow-Deep (p = 0.001*). Species abundance based on summed MaxN of all species present at each site showed...
a similar pattern, with non-significant differences Shallow-Mid (p = 0.47, NS) and Mid-Deep (p = 0.18, NS), and Shallow-Deep was a significant change (p = 0.004*) in pairwise t-tests. Post-hoc Tukey’s HSD Shallow-Mid (p = 0.33, NS), Mid-Deep (p = 0.14, NS) and Shallow-Deep (p = 0.004*). Variation of relative species abundance within depth strata was high, as indicated by standard error (SE) of 27–63% of the mean abundance per depth (Fig. 3). There was also variation in relative species richness within depths, SEs 19–49% mean richness. For both richness and abundance there was a general decrease in the variation between sites from shallow to deep (Fig. 3). However, the variation within strata was not great enough to obscure strong depth-related patterns. The decline in relative species abundance was mirrored in some families, with carangids, labrids and lethrinids decreasing in abundance with depth (Fig. 4). Lutjanidae exhibited depth-related zonation between species, with species *Lutjanus bohar* and *L. sebae* found at shallower depths and species from *Pristipomoides* and *Etelis* genera only in deeper depths. Lethrinidae species *Gymnocranius euanus*, *G. grandoculis* and *Wattsia mossambica* occurred at depths down to 150–160 m, other lethrinid species occurred in 128 m or shallower. Some fish species were only present at depths greater than 100 m (*i.e.* *Pristipomoides aureofasciatus*, *Wattsia mossambica*, *Lipocheilus carnobrumin*, *Paracaeio kusakarii*; Table 1).

**Fish assemblages.** Fish assemblages varied with depth. PCo1 explained 17.5% of the variance and separated the deepest and shallowest sites (Fig. 5a). PCo2 separated the middle sites and explained 11.9% of the variance. Shallower sites (<100 m) were more speciose. *Seriola dumerili, Pristipomoides* species and the lethrinid *Wattsia mossambica* associated with deeper sites. *Lethrinus rubrioperculatus, Gymnocranius euanus, Pentapodus aureofasciatus*, and *Carangoides caeruleopinnatus* frequented shallower sites (Fig. 5b).

There was high species variation within depth strata and a number of single-species occurrences (*i.e.* species only recorded at one site). Fifty-eight species identified were only present in one site, resulting in high among-site diversity. Of single species occurrences, MaxN (the maximum number of a species within a single video frame) ranged from 1–85 individuals.

There were great differences in group membership by depth. However, in some cases there was species overlap in group memberships with depth (Table 3). Indicator species analysis of four pre-defined depth groups and multilevel pattern analysis attributed 130 species to a group or groups based on transformed species abundance. Twenty-three species were selected as having significant differences with depth: 13 were assigned to unique groups and ten species were assigned to two groups. No species were assigned to more than two groups. The upper mesophotic group (54–65 m) had a total of 36 unique species, of which seven were significantly attributed to only that depth strata (p < 0.05). The middle mesophotic group (85–115 m) was assigned 30 species
| Species                  | CAAB code | Australian standard name | Depths observed (Number of videos) | Reported depth range | Depth extension? | Climate and known distribution | New record to the Great Barrier Reef or Australia |
|-------------------------|-----------|--------------------------|------------------------------------|----------------------|------------------|---------------------------------|-----------------------------------------------|
| Carcharhinidae          |           |                          |                                    |                      |                  |                                 |                                               |
| Carcharhinus albimarginatus (Rüppell, 1837) | 37018027 | Silvertip Shark          | 98–155 m (13)                    | 1–800 m             |                  | Tropical Indo-Pacific           | No                                            |
| Carcharhinus amblyrhynchos (Bleeker, 1856) | 37018030 | Grey Reef Shark          | 54–156 m (10)                    | 0–1000 m            |                  | Tropical Indo-West & Central Pacific | No                                            |
| Carcharhinus plumbeus (Nardo, 1827) | 37018007 | Sandbar Shark            | 259 m (1)                        | 0–500 m             |                  | Subtropical Atlantic & Indo-Pacific | No                                            |
| Loxodon macrocephalus Müller & Henle, 1839 | 37018005 | Slitereye Shark          | 107 m (1)                        | 7–100 m             | Marginal         | Tropical Indo-West Pacific      | No                                            |
| Trisaenodon obesus (Rüppell, 1837) | 37018038 | Whitetip Reef Shark      | 54–99.5 m (3)                    | 1–330 m             |                  | Tropical Indo-Pacific           | No                                            |
| Sphyridae               |           |                          |                                    |                      |                  |                                 |                                               |
| Sphyra lewini (Griffith & Smith, 1834) | 37019001 | Scalloped Hammerhead     | 105 m (1)                        | 0–1000 m            |                  | Circumglobal, tropical and temperate seas | No                                            |
| Dasyatidae             |           |                          |                                    |                      |                  |                                 |                                               |
| Taeniura meyeni (Müller & Henle, 1841) | 37035017 | Blotched Fantail Ray     | 54 m (1)                        | 1–500 m             |                  | Tropical Indo-West Pacific      | No                                            |
| Muraenidae             |           |                          |                                    |                      |                  |                                 |                                               |
| Gymnothorax berndti Snyder, 1904 | 37060089 | Y-Patterned Moray*       | 150 m (1)                        | 30–303 m            |                  | West Indo-Pacific               | Yes, new to GBR                               |
| Gymnothorax elegans Bliss, 1883 | 37060090 | Elegant Moray*           | 110–149 m (2)                   | 92–450 m            |                  | Indo-West Pacific               | No, known from unpublished records            |
| Gymnothorax intesi (Fourmanoir & Rivaton, 1979) | 37060076 | Whitetip Moray           | 200 m (1)                       | 200–400 m           |                  | Subtropical West Pacific        | No                                            |
| Gymnothorax prionodon Ogilby, 1895 | 37060049 | Sawtooth Moray           | 150–194 m (2)                   | 20–80 m             | Yes              | Subtropical to temperate West Pacific | No                                            |
| Fistulariidae          |           |                          |                                    |                      |                  |                                 |                                               |
| Fistularia commersonii Rüppell, 1838 | 37278001 | Smooth Flutemouth        | 54 m (1)                        | 0–200 m             |                  | Tropical Indo-Pacific           | No                                            |
| Peristidiidae          |           |                          |                                    |                      |                  |                                 |                                               |
| Serranidae             |           |                          |                                    |                      |                  |                                 |                                               |
| Epinephelus cyanopodus (Richardson, 1846) | 37311145 | Purple Rockcod           | 99.5–102 m (2)                  | 2–150 m             |                  | Tropical West Pacific           | No                                            |
| Epinephelus morrhua (Valenciennes, 1833) | 37311151 | Comet Grouper            | 115–194 m (6)                   | 80–370 m            |                  | Tropical Indo-Pacific           | No                                            |
| Plectropomus leopardus (Lacépède, 1802) | 37311078 | Common Coral Trout       | 100–105 m (2)                   | 3–100 m             | Marginal         | Tropical West Pacific           | No                                            |
| Plectropomus laevis (Lacépède, 1801) | 37311079 | Bluespotted Coral Trout  | 85–128 m (4)                    | 4–100 m             | Yes              | Tropical Indo-Pacific           | No                                            |
| Pseudanthias engelhardii (Allen & Starck, 1982) | 37311115 | Barrier Reef Basslet     | 100 m (1)                       | 37–70 m             | Yes              | Tropical West-Central Pacific   | No                                            |
| Selenastias sp. | 37311947 |                         | 143–179 m (6)                   | 129–204 m           |                  | Subtropical to temperate West Pacific | Yes, new to GBR                               |
| Vairola louti (Forskål, 1775) | 37311166 | Yellowedge Coronation Trout | 54–98 m (2)                     | 3–300 m             |                  | Tropical Indo-Pacific           | No                                            |
| Malacanthidae          |           |                          |                                    |                      |                  |                                 |                                               |
| Hoplostethus marcoi Burgess, 1978 | 37331012 | Redback Sand Tilefish*   | 100 m (1)                       | 18–80 m             | Yes              | Tropical Indo-Pacific           | No                                            |
| Echeneidae             |           |                          |                                    |                      |                  |                                 |                                               |
| Echeneus naucrates Linnaeus, 1758 | 37336001 | Sharksucker              | 54–155 m (8)                    | 0–200 m             | Yes              | Subtropical; Circumtropical     | No                                            |
| Carangidae             |           |                          |                                    |                      |                  |                                 |                                               |
| Carangoides caeruleopinnatus (Rüppell, 1830) | 37337021 | Onion Trevally           | 54–129 m (12)                  | 1–60 m             | Yes              | Tropical Indo-West Pacific      | No                                            |
| Carangoides chrysaphrys (Cuvier, 1833) | 37337011 | Longnose Trevally        | 54–60 m (2)                    | 30–60 m             |                  | Indo-Pacific                    | No                                            |
| Carangoides dinema Bleeker 1851 | 37337078 | Shadow Trevally          | 54–102 m (4)                    | 1–22 m             | Yes              | Tropical Indo-West Pacific      | No                                            |

Continued
| Species | CAAB code | Australian standard name | Depths observed (Number of videos) | Reported depth range | Depth extension? | Climate and known distribution | New record to the Great Barrier Reef or Australia |
|---------|-----------|--------------------------|-----------------------------------|----------------------|----------------|-------------------------------|-----------------------------------------------|
| **Carangoides ferdau** (Forsskål, 1775) | 37337068 | Blue Trevally | 57–100 m (2) | 1–60 m | Yes | Tropical Indo-Pacific | No |
| **Carangoides fulvoguttatus** (Forsskål, 1775) | 37337037 | Turrum | 99.5–102 m (2) | 4–100 m | Marginal | Indo-West Pacific | No |
| **Carangoides orthogrammus** (Jordan & Gilbert, 1882) | 37337057 | Thicklip Trevally | 85–129 m (3) | 3–168 m | No | Tropical Indo-Pacific | No |
| **Caranx plagiopterus** Bleeker, 1857 | 37337070 | Barcheek Trevally | 106 m (1) | 2–200 m | No | Tropical Indo-Pacific | No |
| **Caranx sexfasciatus** Cuvier, 1830 | 37337027 | Giant Trevally | 54–85 m (2) | 10–188 m | No | Tropical Indo-Pacific | No |
| **Caranx melampygus** Cuvier, 1833 | 37337050 | Bluefin Trevally | 54–85 m (2) | 0–190 m | No | Tropical Indo-Pacific | No |
| **Decapterus sp.** | 37337011 |  | 107–155 m (2) |  |  |  |  |
| **Gnathanodon speciosus** (Forsskål, 1775) | 37337012 | Golden Trevally | 102 m (1) | 0–162 m | No | Tropical Pacific | No |
| **Decapterus sp.** | 37337091 |  |  |  |  |  |  |
| **Pseudoceps dentex** (Bloch & Schneider, 1801) | 37337062 | Silver Trevally | 99.5–155 m (2) | 10–238 m | No | Tropical Atlantic and Indo-Pacific | No |
| **Seriola dumerili** (Risso, 1810) | 37337025 | Amberjack | 146–260 m (11) | 1–360 m | No | Sub-tropical, circumglobal | No |
| **Seriola rivoliana** Valenciennes, 1833 | 37337052 | Highfin Amberjack | 98–245 m (10) | 5–250 m | No | Sub-tropical, circumglobal | No |

**Lutjanidae**

| Species | CAAB code | Australian standard name | Depths observed (Number of videos) | Reported depth range | Depth extension? | Climate and known distribution | New record to the Great Barrier Reef or Australia |
|---------|-----------|--------------------------|-----------------------------------|----------------------|----------------|-------------------------------|-----------------------------------------------|
| **Aphareus rutilans** Cuvier, 1830 | 37346001 | Rusty Jobfish | 85–245 m (23) | 10–330 m | No | Tropical Indo-Pacific | No |
| **Aprion virens** Valenciennes, 1830 | 37346027 | Green Jobfish | 54–105 m (2) | 0–180 m | No | Tropical Indo-Pacific | No |
| **Etelis carunculatus** Cuvier, 1828 | 37346014 | Ruby Snapper | 226 m (1) | 90–400 m | No | Tropical Indo-Pacific | No |
| **Lipochilus cariosbromus** (Chan, 1970) | 37346031 | Tang's Snapper | 194 m (1) | 90–340 m | No | Indo-West Pacific | No |
| **Lutjanus bohar** (Forsskål, 1775) | 37346029 | Red Bass | 85–128 m (10) | 4–180 m | No | Tropical Indo-Pacific | No |
| **Lutjanus sebae** (Cuvier, 1816) | 37346004 | Red Emperor | 99.5–103 m (2) | 5–180 m | No | Tropical Indo-West Pacific | No |
| **Paraceto kusakarii** Abe, 1960 | 37346060 | Saddleback Snapper | 156–200 m (3) | 100–310 m | No | Tropical West Pacific | No |
| **Pristipomoides argyrogrammicus** (Valenciennes, 1831) | 37346054 | Ornate Jobfish | 193–245 m (6) | 70–350 m | No | Tropical Indo-Pacific | No |
| **Pristipomoides auricilla** (Jordan, Evermann & Tanaka, 1927) | 37346059 | Goldflag Snapper | 150–194 m (3) | 90–360 m | No | Indo-Pacific | No |
| **Pristipomoides filamentosa** (Valenciennes, 1830) | 37346032 | Rosy Snapper | 85–201 m (16) | 40–400 m | No | Indo-Pacific | No |
| **Pristipomoides multisens** (Day, 1870) | 37346002 | Goldbanded Snapper | 129–250 m (14) | 40–350 m | No | Tropical & sub-tropical Indo-Pacific | No |
| **Pristipomoides seboldii** (Bleeker, 1857) | 37346064 | Lavender Snapper | 143 m (1) | 100–500 m | No | Indo-Pacific | No |
| **Pristipomoides typus** Bleeker, 1852 | 37346019 | Sharptooth Snapper | 115–250 m (18) | 40–180 m | Yes | Tropical Indo-Pacific | No |
| **Symphorus nematophorus** (Bleeker, 1860) | 37346017 | Chinamanfish | 60–105 m (4) | 20–100 m | Marginal | Tropical West Pacific | No |

**Caesionidae**

| Species | CAAB code | Australian standard name | Depths observed (Number of videos) | Reported depth range | Depth extension? | Climate and known distribution | New record to the Great Barrier Reef or Australia |
|---------|-----------|--------------------------|-----------------------------------|----------------------|----------------|-------------------------------|-----------------------------------------------|
| **Pterocaesio marri** Schultz, 1953 | 37346068 | Bigtail Fusilier | 54 m (1) | 1–35 m | No | Tropical Indo-Pacific | No |

**Sympyrsodonidae**

| Species | CAAB code | Australian standard name | Depths observed (Number of videos) | Reported depth range | Depth extension? | Climate and known distribution | New record to the Great Barrier Reef or Australia |
|---------|-----------|--------------------------|-----------------------------------|----------------------|----------------|-------------------------------|-----------------------------------------------|
| **Symphyrsodon sp.** | 37346030 |  | 115 m (1) |  |  |  |  |

**Nemipteridae**

| Species | CAAB code | Australian standard name | Depths observed (Number of videos) | Reported depth range | Depth extension? | Climate and known distribution | New record to the Great Barrier Reef or Australia |
|---------|-----------|--------------------------|-----------------------------------|----------------------|----------------|-------------------------------|-----------------------------------------------|
| **Nemipterus balinensis** (Bleeker, 1859) | 37347039 | Bali Threadfin Bream | 194–240 m (2) | 50–150 m | Yes | Tropical Indo-West Pacific | No |
| **Pentapodus aureofasciatus** Russell, 2001 | 37347029 | Yellowstripe Threadfin Bream | 54–106 m (7) | 5–80 m | Yes | Tropical Pacific | No |
| **Pentapodus nagasakiensis** (Tanaka, 1915) | 37347012 | Japanese Threadfin Bream | 100 m (1) | 2–100 m | No | Tropical West Pacific | No |

Continued
| Species | CAAB code | Australian standard name | Depths observed (Number of videos) | Reported depth range | Depth extension? | Climate and known distribution | New record to the Great Barrier Reef or Australia |
|---------|-----------|--------------------------|-----------------------------------|----------------------|-----------------|-------------------------------|-----------------------------------------------|
| Scolopsis sp. | 37347902 | 65 m (1) | | | | | |
| **Lethrinidae** | | | | | | | |
| Gymnocranius euanus (Gunther, 1879) | 37351022 | Paddletail Seabream | 54–156 m (10) | 15–50 m | Yes | Tropical West Pacific | No |
| Gymnocranius granoculis (Valenciennes, 1830) | 37351005 | Robinson's Seabream | 54–155 m (10) | 20–170 m | Tropical Indo-Pacific | No |
| Lethrinus laticeps Alleyne & Macleay, 1877 | 37351006 | Grass Emperor | 54 m (1) | 5–35 m | Yes | Tropical West Pacific | No |
| Lethrinus miniatus (Forster, 1801) | 37351009 | Redthroat Emperor | 54–128 m (8) | 5–250 m | Yes | Tropical West Pacific | No |
| Lethrinus nebulosus (Forsskål, 1775) | 37351008 | Spangled Emperor | 100–179 m (2) | 0–90 m | Yes | Tropical Indo-West Pacific | No |
| Lethrinus olivaceus Valenciennes, 1830 | 37351004 | Longnose Emperor | 54–105 m (5) | 1–185 m | Yes | Tropical Indo-West Pacific | No |
| Lethrinus rubripersculatus Sato, 1978 | 37351012 | Drab Emperor | 54–128 m (5) | 5–35 m | Yes | Tropical West Pacific | No |
| Lethrinus semicinctus Valenciennes, 1830 | 37351016 | Blackblotch Emperor | 54 m (1) | 4–35 m | Yes | Tropical Indo-West Pacific | No |
| Lethrinus sp. | 37351027 | Mozambique Seabream | 105–160 m (8) | 100–300 m | Yes | Tropical Indo-West Pacific | No |
| **Mullidae** | | | | | | | |
| Mulloludichthys pfluegeri (Steindachner, 1900) | 37355040 | Orange Goatfish | 54–103 m (3) | 13–200 m | Tropical Indo-West Pacific | Yes |
| Parupeneus hepactanaxis (Lacépède, 1802) | 37355004 | Cinnabar Goatfish | 54–103 m (4) | 12–350 m | Tropical Indo-West Pacific | No |
| Parupeneus multifasciatus (Quoy & Gaimard, 1825) | 37355026 | Banded Goatfish | 54 m (1) | 3–161 m | Tropical Pacific | No |
| Parupeneus pleurostigma (Bennett, 1831) | 37355027 | Sidespot Goatfish | 100 m (1) | 1–120 m | Tropical Indo-Pacific | No |
| **Chaetodontidae** | | | | | | | |
| Heniochus diphreutes Jordan, 1903 | 37365005 | Schooling Bannerfish | 128 m (1) | 5–210 m | Subtropical Indo-Pacific | No |
| **Pomacentridae** | | | | | | | |
| Pomacentrus imperator (Bloch, 1787) | 37365014 | Emperor Angelfish | 100–105 m (2) | 1–100 m | Tropical Indo-Pacific | No |
| Pomacentrus semicirculatus (Cuvier, 1831) | 37365080 | Blue Angelfish | 105 m (1) | 1–40 m | Yes | Tropical Indo-West Pacific | No |
| **Cirrhitidae** | | | | | | | |
| Cirrhitus polyactis Bloch, 1802 | 37374006 | Lyretail Hawkfish | 100 m (1) | 10–132 m | Tropical Indo-West Pacific | No |
| **Pomacentridae** | | | | | | | |
| Chromis circumastrea Pyle, Earle & Greene, 2008 | 37372153 | Gold-rim Chromis* | 115 m (1) | 7–100 m | Yes | Tropical West Pacific | Yes |
| Chromis mirabilis Tanaka 1917 | 37372048 | Japanese Puller | 155–194 m (2) | 40–208 m | Subtropical West Pacific | Yes, new to GBR |
| Chromis okamurai Yamakawa & Randall, 1989 | 37372154 | Okinawa Chromis* | 143 m (1) | 135–175 m | Subtropical to temperate Northwest Pacific | Yes |
| Chromis sp. | 37372155 | | 155 m (1) | | | Potential new species | |
| **Labridae** | | | | | | | |
| Bodianus anthioides (Bennett, 1832) | 37384052 | Lyretail Pigfish | 54 m (1) | 6–60 m | Tropical Indo-Pacific | No |
| Bodianus bimaculatus Allen, 1973 | 37384055 | Twospot Pigfish | 100–106 m (2) | 30–70 m | Yes | Tropical Indo-Pacific | No |
| Bodianus izuensis Araga & Yoshino, 1975 | 37384058 | Striped Pigfish | 98–105 m (2) | 12–70 m | Yes | Subtropical West Pacific | Yes |
| Bodianus massulai Araga & Yoshino, 1975 | 37384221 | | 115–155 m (2) | 30–113 m | Yes | Subtropical: West Pacific antitropical distribution | Yes |

Continued
| Species                  | CAAB code | Australian standard name                  | Depths observed (Number of videos) | Reported depth range | Depth extension? | Climate and known distribution                                      | New record to the Great Barrier Reef or Australia |
|-------------------------|-----------|-------------------------------------------|-----------------------------------|----------------------|------------------|---------------------------------------------------------------------|--------------------------------------------------|
| Bodianus bennetti       | 37384219  | Lemon-striped Pygmy Hogfish              | 155–179 m (4)                    | 97–130 m             | Yes              | West Pacific                                                      | Yes, new to GBR, recently published record from the Coral Sea |
| Bodianus sp. 1          | 37384220  |                                            | 143 m (1)                        |                      |                  |                                                                     | Potential new species                              |
| Cheilinus undulatus     | 37384038  | Humphead Maori Wrasse                     | 54 m (1)                         | 1–100 m              |                  | Tropical Indo-Pacific                                              | No                                                |
| Choerodon venustus      | 37384042  | Venus Tuskfish                            | 54 m (1)                         | 10–95 m              |                  | Subtropical West Pacific                                           | No                                                |
| Cirrhilabrus punctatatus| 37384083  | Finespot Wrasse                           | 54–85 m (2)                      | 2–78 m               | Yes              | Tropical West Pacific                                              | No                                                |
| Cirrhilabrus roseaflavus| 37384218  | Pink-Banded Fairy Wrasse*                 | 85–155 m (8)                     | 30–100 m             | Yes              | Tropical West Pacific                                              | Yes, new to GBR, recently published record from the Coral Sea |
| Cirrhilabrus sp.        | 37384910  |                                            | 54–200 m (2)                     |                      |                  |                                                                     |                                                   |
| Corydoradus forsteri     | 37384093  | Pinklined Wrasse                          | 60 m (1)                         | 2–45 m               | Yes              | Tropical West Pacific                                              | No                                                |
| Halichoeres sp.         | 37384920  |                                            | 54 m (1)                         |                      |                  |                                                                     |                                                   |
| Labroides dimidiatus    | 37384028  | Common Cleanerfish                        | 54 m (1)                         | 1–40 m               |                  | Tropical Indo-Pacific                                              | No                                                |
| Labridae sp.            | 37384000  |                                            | 54 m (1)                         |                      |                  |                                                                     |                                                   |
| Oxycheilinus digrammus  | 37384065  | Violetline Maori Wrasse                   | 179–193 m (2)                    | 3–120 m              | Yes              | Tropical Indo-Pacific                                              | No                                                |
| Oxycheilinus orientalis | 37384030  | Oriental Maori Wrasse                     | 99.5–110 m (2)                   | 10–80 m              | Yes              | Tropical Indo-West Pacific                                         | No                                                |
| Oxycheilinus sp.        | 37384933  |                                            | 150 m (1)                        |                      |                  |                                                                     |                                                   |
| Terelabrus rubrovittatus | 37384210  | Yellowbar Hogfish*                        | 100–179 m (8)                    | 50–140 m             | Yes              | Tropical Western Central Pacific; Japan; Maldives                   | Yes                                               |

**Table 1.** Fish species identified in deep-reef Baited Remote Underwater Video Station videos from the Central Great Barrier Reef shelf-break. Identifications to species designation where possible and taxonomic information.
based on the Australian Faunal Directory\textsuperscript{58} and California Academy of Sciences’ Catalog of Fishes\textsuperscript{59}. CAAB codes are the eight-digit Codes for Australian Aquatic Biota maintained by CSIRO Division of Marine and Atmospheric Research for species of research or commercial interest. Australian standard names are according to the Australian Faunal Directory or *FishBase\textsuperscript{60} common name. FishBase, Fishes of Australia\textsuperscript{61}, IUCN Redlist\textsuperscript{54}, Randall’s Reef and Shore Fishes of the South Pacific,\textsuperscript{62} and Allen and Erdmann’s Reef Fishes of the East Indies app\textsuperscript{63} were consulted for reported depth range. Where differences in these references occurred, the maximum depth range is reported. Climate and known distribution information from FishBase. New record information was compared to reported data from FishBase, Fishes of Australia and Atlas of Living Australia\textsuperscript{64} databases and cross-referenced with John Pogonoski (CSIRO).

with three significant. The lower mesophotic (128–160 m) had 18 species assigned, two were significant. The sub-mesophotic group (179–260 m) was assigned 13 species, only one was significant. There was a greater shared assemblage between the upper and middle mesophotic (11 species total), then between the upper and lower or the upper and sub-mesophotic groups. Middle and lower-mesophotic shared 11 species; the lower mesophotic and sub-mesophotic sites shared six species. The genus Parapercis (Family Pinguipedidae) was unusual in that it may be a depth-generalist genus, found in all three mesophotic groups (0.462, \( p = 0.765 \)). Further, the highly mobile Gymnosarda unicolor (Family Scombridae) was found throughout the deepest groups (0.622, \( p = 0.363 \)). Presence-absence data revealed almost identical results, out of 130 species 24 were selected: 12 were assigned to a unique group, 12 assigned to pairs of groups.

**Discussion**

We found strong differences in fish assemblages with depth with high variability among reefs and sites within reefs. Further, we found distinct assemblages of fishes in mesophotic and sub-mesophotic habitats of the GBR, and these contrasted greatly with those of shallower shelf-habitats (e.g. soft bottom 20–90 m\textsuperscript{37,65}), including those of coral reefs (<30 m)\textsuperscript{66–68}. There are few comprehensive datasets on tropical deep-reef fishes, however, there is a growing body of comparable work in disparate locations, such as Hawaii, Brazil, Puerto Rico and the Caribbean. Our study is the first to characterize the diversity of deep-reef fish assemblages in the GBR. These depth patterns are similar to other deeper marine systems where the fish community shows strong zonation and declining species richness and abundance with the depth gradient (e.g. refs\textsuperscript{19,36,49,69–71}). Some species show narrower depth ranges, while others are less restricted, and this has important implications for the future management of these resources. For instance, conservation planners can set aside representative areas based on depth to maximize protection of mesophotic reefs and species. Fishery managers can better define optimal targeted fishing depths and designate “Essential Fish Habitat” based on depth\textsuperscript{72}, such as the designated Bottomfish Restricted Fishing Areas (BRFAs) implemented in the Hawaiian Bottomfish Fishery, for the protection of commercially important deep-reef fishes\textsuperscript{46,52,53,73,74}.

Fisheries are vulnerable to the effects of fishing if there is limited habitat or constrained depth-ranges for target species. Shallow waters have been heavily impacted by fishing\textsuperscript{75}. In the tropics, where the food security of many countries is uncertain, deeper reefs may be next in-line for greater fishing pressure. Many tropical coastlines that have limited shallower fishing areas are targeting deeper fisheries\textsuperscript{76}. This is concerning as deeper environments are thought to be vulnerable\textsuperscript{5,76,77} and fish assemblages are poorly described\textsuperscript{78,79}, which may compound the problem. In general, deeper fish assemblages are thought to be diverse, valuable and vulnerable\textsuperscript{80}. Since many of these species only occur at deeper depths, it is critical to consider these depth zones as distinct. Bycatch is one of the immeasurable impacts of fishing, therefore, it is important to inventory the biodiversity and value we may lose when we target deeper fisheries. High single-species occurrences can indicate the relative rarity of the fish taxa, but this can only be answered with future sampling and greater spatial replication. It is imperative, therefore, to obtain thorough baseline information on deeper tropical ecosystems before these species and habitats are compromised.

Some of the key indicator species per depth strata were commercially important species. Deep Lutjanidae (snappers from the genera Apherines, Etilis and Pristipomoides), serranids, carangids and sharks are among the “largely unexplored fauna” of the Townsville area and continental slope\textsuperscript{81}, and important for “regional food futures”\textsuperscript{82}. Australia shares fauna with the south-western Pacific islands and the larger Indo-Pacific region\textsuperscript{83}. As human populations increase across Australia and Indo-Pacific islands nations, pressure will be added to fish stocks throughout the region and sustainable fisheries management will increasingly become a major international political issue\textsuperscript{81–83}.

In many Pacific nations, there are long-standing and emerging deep bottomfish fisheries and there is growing concern that these data-limited fisheries are vulnerable to the effects of overfishing\textsuperscript{7,84,85}. In Hawaii, deep-reef lutjanids, serranids and carangids form the second largest fishery behind the tuna fishery\textsuperscript{86}. For the majority of these fishes, biological information is lacking, but limited life history information demonstrate overall low production (see review\textsuperscript{86}). “Essential Fish Habitat” has been set aside to reduce the impacts from fishing in Hawaiian waters\textsuperscript{87} and in other countries where these species are targeted similar precautionary measures should be made.

In Australia, deep-reef fishes are targeted by multiple methods along an extensive tropical coastline spanning Queensland, the Australian and the Northern Territory. In the Northern Territory and Western Australia, mixed gear is used to target Pristipomoides species, primarily Pristipomoides multisetus\textsuperscript{87,88}; however, often multiple species are marketed under the same common name “Goldband snapper”\textsuperscript{89}. In Western Australian waters deepwater demersal trawl gear is also used to target deep-reef fishes\textsuperscript{90}. Fishing methods which target >50 species in ~200 m depths unfortunately catch many species as bycatch. In Queensland, while fishing pressure in deeper habitats of the GBR is comparatively lower than in shallow waters, more comprehensive information on deeper
habitats will help to extend conservation strategies for the GBR World Heritage Area\(^{35,91}\) and the adjacent Coral Sea\(^{39,41}\) to incorporate deeper habitats.

Variation in fish assemblages was strongly correlated with depth and a combination of biotic and abiotic environmental conditions may contribute to this pattern. The thermocline and changing temperature and productivity with depth, may correlate with food for planktivores and piscivores\(^{85,93}\). Position of the thermocline is probably a key factor driving the distribution of fishes\(^5,94\). Our CTD data indicate temperatures rapidly decline below 100 m to 150–200 m, and similar profiles have been previously recorded in this area\(^{95}\); a steeper change than recorded in other tropical mesophotic regions\(^3,5,94\). This depth corresponds with a transition from the lower mesophotic assemblage to the sub-mesophotic fishes. Variation in physical properties (i.e., nutrients, light, oxygen and temperature) of the water column along with position and intensity of the thermocline influence species abundances in shallow tropical waters\(^96,97\) and this appears to apply in deep shelf-waters\(^98\). Competition is also a powerful influence on species richness and abundance in shallower waters\(^99–101\) and more research on mesophotic competitive interactions is needed.

We found strong patterns of fish abundance with depth, but there was also some variation among reefs that may reflect depth-related patterns of habitat structural complexity\(^102–104\). Decreases or changes in fish diversity within depth strata may be linked to differences in available habitat similar to shallow water environments\(^5,105–108\). Environmental drivers, such as currents and thermal stratification, will affect physical characteristics of the environment (i.e., temperature, sedimentation and food availability), which influence abundance and species diversity\(^109\). These abiotic factors affect the benthic community (the biotic structures, e.g., hard coral), which combined with the geomorphology, constitutes the habitat available to fishes\(^110\). Our results indicate inter-reefal habitats had lower relative species richness than those neighbouring reefs, suggesting the importance of the habitat type on diversity. Habitat quality may also explain some variation in relative species richness and abundance among reefs sampled.

Of the information necessary for conservation strategies, worldwide current species inventories and distributions are incomplete\(^111\). Further, data-poor locations inhibit the ability to monitor and record range extensions and distributional records. Analogous to the tropicalization of temperate waters\(^112,113\), shallower species may extend their range and begin to inhabit deeper depths\(^114\). There is little information on how thermal tolerances may change fish distributions or behavior, such as changing spawning locations or moving deeper to avoid warm waters\(^6\). Distributional records and documented range extensions can be used as a "canary in a coalmine", fishes as sentinel species can indicate the relative health of the broader ecosystems.

|                  | DF | SS  | MS  | F-value | p   |
|------------------|----|-----|-----|---------|-----|
| **Richness**     |    |     |     |         |     |
| Among depths     | 2  | 12.55 | 6.28 | 7.19    | 0.002* |
| Within depths    | 39 | 34.04 | 0.87 |         |     |
| **Abundance**    |    |     |     |         |     |
| Among depths     | 2  | 38.62 | 19.31 | 5.88    | 0.006* |
| Within depths    | 39 | 128.13 | 3.29 |         |     |

Table 2. Species richness and abundance decreased with depth across all reefs pooled (one-way ANOVA).
Shelf-break environments may be priority conservation hotspots, with high proportions of endemics\textsuperscript{21, 22} or species with restricted depth-ranges\textsuperscript{33, 115}. Australia has high total endemism and up to a third of its demersal fishes may be endemic\textsuperscript{30}, therefore, there may also be high endemism in its demersal shelf-break fish assemblages. We may also be underestimating the Australian shelf-break’s conservation value, as key bioregions including the upper continental slope of Queensland and the inter-reefal areas of the GBR are missing comprehensive fish assemblage information\textsuperscript{31}. As genetic tools are increasing the resolution of cryptic speciation, there are likely differences detected between eastern and western Australian populations, and within species-complexes from neighboring regions\textsuperscript{30}. Even without this information, Last \textit{et al.} (2005, 2011) concluded that Australia-wide...
Table 3. Key fish indicator species per depth strata (multilevel pattern analysis). IndVal index (0–1) is accompanied by significance levels: *p ≤ 0.05, **p ≤ 0.01, ***p ≤ 0.001; †a for species abundance data, ‡o for occurrence (presence-absence) data.

| Species which contribute significantly to each group | Upper mesophotic (54–45, n = 4) | Middle mesophotic (85–115 m, n = 14) | Lower mesophotic (128–160 m, n = 15) | Sub-mesophotic (179–200 m, n = 15) |
|----------------------------------------------------|-------------------------------|-------------------------------|-------------------------------|-------------------------------|
| Lethrinus rubripunctatus 0.752 ** a,o               |                               |                               |                               |                               |
| Latijanus bohar 0.774 ** a,o                        |                               |                               |                               |                               |
| Pseudocaranx dentatus 0.691 * a,o                   |                               |                               |                               |                               |
| Gymnocranius brachyura 0.672 * a                   |                               |                               |                               |                               |
| Abalistes stellatus 0.957 *** a,o                  |                               |                               |                               |                               |
| Lethrinus rubripunctatus 0.752 ** a                 |                               |                               |                               |                               |
| Latijanus bohar 0.774 ** a                          |                               |                               |                               |                               |
| Pseudocaranx dentatus 0.691 * a                     |                               |                               |                               |                               |
| Gymnocranius brachyura 0.672 * a                    |                               |                               |                               |                               |
| Lethrinus rubripunctatus 0.752 ** a                 |                               |                               |                               |                               |
| Latijanus bohar 0.774 ** a                          |                               |                               |                               |                               |
| Pseudocaranx dentatus 0.691 * a                     |                               |                               |                               |                               |
| Gymnocranius brachyura 0.672 * a                    |                               |                               |                               |                               |
| Lethrinus rubripunctatus 0.752 ** a                 |                               |                               |                               |                               |
| Latijanus bohar 0.774 ** a                          |                               |                               |                               |                               |
| Pseudocaranx dentatus 0.691 * a                     |                               |                               |                               |                               |
| Gymnocranius brachyura 0.672 * a                    |                               |                               |                               |                               |
| Lethrinus rubripunctatus 0.752 ** a                 |                               |                               |                               |                               |
| Latijanus bohar 0.774 ** a                          |                               |                               |                               |                               |
| Pseudocaranx dentatus 0.691 * a                     |                               |                               |                               |                               |
| Gymnocranius brachyura 0.672 * a                    |                               |                               |                               |                               |
| Lethrinus rubripunctatus 0.752 ** a                 |                               |                               |                               |                               |
| Latijanus bohar 0.774 ** a                          |                               |                               |                               |                               |
| Pseudocaranx dentatus 0.691 * a                     |                               |                               |                               |                               |
| Gymnocranius brachyura 0.672 * a                    |                               |                               |                               |                               |
| Lethrinus rubripunctatus 0.752 ** a                 |                               |                               |                               |                               |
| Latijanus bohar 0.774 ** a                          |                               |                               |                               |                               |
| Pseudocaranx dentatus 0.691 * a                     |                               |                               |                               |                               |
| Gymnocranius brachyura 0.672 * a                    |                               |                               |                               |                               |
| Lethrinus rubripunctatus 0.752 ** a                 |                               |                               |                               |                               |
| Latijanus bohar 0.774 ** a                          |                               |                               |                               |                               |
| Pseudocaranx dentatus 0.691 * a                     |                               |                               |                               |                               |
| Gymnocranius brachyura 0.672 * a                    |                               |                               |                               |                               |

In conclusion, we found that depth was a strong predictor of fish assemblages at mesophotic and sub-mesophotic depths of the GBR. Our findings on the GBR align with other tropical and sub-tropical studies in deeper habitats. Distinct fish assemblages and high species diversity was found along the depth gradient and this potentially contributes to high levels of endemism in Australian fishes and other parts of the world. These narrow depth distributions may constitute an inherent vulnerability to targeted fishing pressures and should be incorporated in future regional management strategies.
individuals of a species per frame) reached, until the end of sampling (when the video left the bottom or when the tape finished recording). MaxN is a conservative estimate of abundance to eliminate the possibility of re-counting fish swimming in and out of the field-of-view65. Videos were read to its full length (27 to 84 minutes, average soak of 54 minutes) and later standardized for length of time of sampling (number of species present-absent per site for species richness, and number of fish per species for relative abundance, per 60 minute increment). Fish were identified to lowest possible taxa, with the assistance of fish experts, fish identification books and FishBase.org60. Every effort was made to identify large, conspicuous fish in addition to smaller, cryptic species. Fish identification photographs and BRUVS deployment metadata are archived in the Australian Institute of Marine Science database and can be accessed by request.

**Depth patterns.** Species were summed across all sites for species richness and abundance. Where standardized values of total abundance and richness were used, the estimates were standardized by number of species per 60 minutes of sampling time. For our analyses two depth classification systems were used. For the one-way ANOVA which required a balanced design, three depth categories "Shallow" (50–115 m), "Mid" (128–160 m) and "Deep" (179–260 m) were used. For other analyses "Shallow" was further divided to two smaller categories to investigate the differences 50–115 m. Our sites were categorized in four depth strata: “upper mesophotic” (50–65 m), “middle mesophotic” (85–115 m), “lower mesophotic” (128–160 m) and “sub-mesophotic” (179–260 m). These strata represented breaks in the depth-stratified sampling design, but also aligned with previously documented transitional boundaries, including the ~150 m lower depth-limit of Mesophotic Coral Ecosystems (MCEs)135. Analyses were performed using several packages in R statistical software132,133 (CRAN ver. 3.2.3) and Excel.

To evaluate the general trend of how species richness and abundance varied with depth, standardized richness and abundance were square-root transformed and data were tested for any significant deviation from normality (Shapiro-Wilks: species richness Wilks = 0.98, p = 0.66; abundance Wilks = 0.95, p = 0.07) to meet the assumptions of ANOVA. In our original design we had the factors ‘Depth’ (a = 3) and ‘Reef’ (b = 3; Myrmidon, Unnamed, Viper) and site (n = 4) with an interaction between depth and site. The interaction was weak (p < 0.25), therefore, the factors were pooled as recommended by Underwood (1997)131. The factor ‘Reef’ was pooled for a stronger test for the factor ‘Depth’. ANOVA was performed for Depth (a = 3, n = 14) for both richness and abundance and two-tailed t-tests between depth groups with a Bonferroni correction was applied.

Mean standardized richness and abundance were also plotted in relation to depth strata separately by reef (Myrmidon, Viper and Unnamed; varied number of replicates within stratum). In addition, deployments were made along an inter-reefal transect (60–200 m, one replicate per depth). Shallower BRUVS sets from Viper Reef, one from on top of the submerged unnamed deep reef and the inter-reefal transect were included as an additional (50–65 m depth strata, n = 4). For analysis of separate families, we separated the Lutjanidae family into “deep” members (Etelis and Pristipomoides genera) and “other” (all other member species). Family analyses followed the one-way ANOVA for species richness and abundance.

**Investigating fish assemblages.** We also wanted to investigate species associations as they may be better predictors of environmental conditions than species individually. This is often difficult because of positively-skewed frequency distributions and the high frequency of zeros in larger community composition datasets132. Species abundances (summed MaxN, maximum number of fish per species per site) were fourth-root transformed, which down-weights highly abundant species and reduces the skew in the distribution for each species133.

We used a Principle Coordinate Analysis (PCoA) ordination to visualise the differences between sites. Eliminating single-species occurrences (species only occurring at one site) from this analysis (58 of 130 species), we used 47 of the sites with 72 of the fish species in a Bray-Curtis dissimilarity matrix (packages vegan134, ecodist135). Agglomerative hierarchical unconstrained clustering revealed 12 significant clusters (SIMPROF; packages cluster136, clustersig137). For the ordination we color-coded the sites with the depth strata from the previous constrained univariate analyses and size-coded the symbols to correspond with species richness in the resulting biplot (functions capscale, vegdist). Capscale revealed ordination distances that were analogous to the original dissimilarities and is similar to redundancy analysis but can utilise non-Euclidean dissimilarities134. To determine which fish species corresponded with the variance between sites, we plotted the 15 species with the highest species scores.

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**Measurements of temperature with depth.** On the outer shelf-edge off Myrmidon Reef, near the 300 m isopleth (Fig. 1), a Seabird Conductivity Temperature and Depth recording device was slowly lowered (<1 m/sec)
by hand to an estimated maximum depth before retrieval. The instrument was calibrated for 60 seconds below the surface before deployment. Repeated samples were made in early August 2009, 2010 and 2013. All methods in this study were carried out in accordance with local guidelines and regulations for the GBRMP. Experimental protocols were approved by the animal ethics committee at James Cook University. Methods were non-invasive and no animals were taken in this fieldwork.

**Data availability statement.** BRUVS deployment information, recorded species and linked images are available by request from the Australian Institute of Marine Science. Map bathymetric contour lines from Dr. Rob Beaman and Project 3D GBR (www.deepref.org); map shapefiles provided by the Great Barrier Reef Marine Park Authority (http://www.gbrmpa.gov.au/resources-and-publications/spatial-data-information-services).

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**Author Contributions**

T.S., M.C. and M.J.K. conceived the study. T.S. and M.J.K. conducted the fieldwork. T.S. analyzed the videos, compiled the dataset and performed statistical analyses. M.C. checked species identification and offered assistance with the database and statistical methods. M.C. and T.S. commissioned the illustrations drawn by Juliet Corley. All authors contributed to the manuscript.

**Additional Information**

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