

# A Large Aggregation of Liparids at 7703 meters and a Reappraisal of the Abundance and Diversity of Hadal Fish

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*Few biological studies have investigated the hadal depths within oceanic trenches that plummet from 6000 meters (m) to the full ocean depth of almost 11,000 m. Here we present the deepest known in situ observations of fish: a hadal snailfish, *Pseudoliparis amblystomopsis* (Andriashev 1955), from 7703-m deep in the Japan Trench, which was obtained using a baited video lander. The maximum number of fish we observed was unexpectedly higher than trawl catch records of any known hadal fish. We describe changes in fish abundance and associated behaviors over time, including feeding, resting, and swimming. In light of these new observations, we reappraise the occurrence and diversity records of hadal fishes that have been constructed from fragmentary and often misleading information derived from historical explorations and global data sets. This reappraisal suggests that hadal fish diversity may be lower—although some hadal fish species may attain much larger populations—than previously thought.*

*Keywords: deep-sea fish, hadal trench, Liparidae, baited lander, bathyscaphe*

**T**he extents of the horizontal spatial patterns and vertical depth ranges of fish occurrence in deep-sea trenches remain unresolved. Although fishes of the abyssal zone (3000–6000 m) are well documented across world oceans (Merrett and Haedrich 1997), records of fishes in the hadal zone (6000–11,000 m) are comparatively less numerous, and their population assessments are complicated by assumptions made on the basis of sparse historical data (Wolff 1961, Nielsen 1964). Building an adequate hadal record has been hampered by the technical challenges and infrequency of sampling at such extreme depths. Inconsistency in sampling methods and a low number of unreplicated samples also make it difficult to accurately assess population structure or confidently explain population dynamics. In this article, we briefly review historical findings of hadal-occurring fishes, and compare these with new observations obtained using noninvasive imaging technology from our recent hadal trench expedition. We reanalyzed hadal fish records and reappraised global archived data sets to advance the current understanding of the occurrence and diversity of hadal fish species, revealing new issues and future directions for research in deep-sea fish ecology.

## Historical findings of hadal fish species

The first fish from hadal depths was sampled in 1901 by the *Princess Alice* in the eastern Atlantic Ocean. This ophidiid (cusk eel), *Bassogigas profundissimus* (Roule 1913), held the “deepest fish” record (6035 m) until the Danish *Galathea* expedition in 1950–1952 trawled another specimen from the Sunda (Java) Trench at 7160 m in the northeastern Indian Ocean. The *Galathea* also collected five liparids (snailfish) of the species *Careproctus kermadecensis* (Nielsen 1964) in one haul between 6660 m and 6770 m in the Kermadec Trench in the southwestern Pacific Ocean. Two additional liparid species were then caught by bottom trawling during the Russian *Vityaz* expeditions (1953–1957) in the northwestern Pacific Ocean: an individual *Careproctus amblystomopsis* (Andriashev 1955) from 7230 m in the Kuril-Kamchatka Trench; and another individual, a species of *Careproctus*, from 7579 m in the Japan Trench. These two specimens were later reclassified as *Notoliparis (C) kermadecensis* (Nielsen 1964) and *Pseudoliparis (C) amblystomopsis*, respectively.

In 1970, a third specimen of *B. profundissimus* was collected at 8370 m in the Puerto Rico Trench, in the northwestern Atlantic Ocean (Staiger 1972). This specimen, later reclassified as *Abyssobrotula galathea* (Nielsen 1977),

is generally considered the deepest-living fish collected, although the issue of pelagic or demersal origin has never been unequivocally resolved. Since this account, several other hadal fish specimens have been described (e.g., Anderson et al. 1985, Nielsen et al. 1999, Chernova et al. 2004, Stein 2005), but because it is difficult to ascertain precise depth when specimens are captured by a nonclosing trawl haul, many of these observations lack confidence.

Perhaps the most popular alleged account of the deepest living fish concerns the reports from bathyscaphe dives in the 1960s. On 23 January 1960, the crew of the *Trieste* dived to the deepest point on Earth (Challenger Deep, 10,912 m; Mariana Trench, western Pacific) and reported seeing a “flatfish” that was “white and about a foot long” (Piccard and Dietz 1961). Although there was no photographic evidence to substantiate these claims, this information was publicized widely, but was discredited shortly thereafter by Wolff (1961), who suggested that the flatfish was more likely to be a holothurian, as flatfish are rarely found beyond continental shelf and slope—a sentiment also reiterated by Nielsen (1964). Even the possibility of a similarly shaped fish such as a ray or skate inhabiting these depths is unlikely (Priede et al. 2006).

A more credible report around the same period, however, came from the French *Archimède* bathyscaphe while transecting the Puerto Rico Trench at 7300 m; the team observed 200 small fish similar to *Careproctus* species (family: Liparidae) and three individuals belonging to two other fish species (Pérès 1965). Although these observations are intriguing (they describe a high abundance of fish at hadal depths that did not correspond to trawl catch records of any known hadal fish), as with the observations made by during the *Trieste* dives, no photographic evidence was available to corroborate the claim.

Current understanding of the occurrence of hadal fishes comes from a very limited number of fish specimens recovered from conventional trawl sampling. Given that most of the known hadal fish species have been described from single, isolated finds, or from repeated but occasional finds, population sizes of hadal fishes have been assumed to be extremely low, diminishing with depth, with solitary individuals inhabiting food-sparse environments. Although the lower vertical distributional limit of around 8000 m generally agrees with more recent *in situ* observations of hadal populations (Jamieson et al. 2009a), as well as recent global depth-related regressions (Priede et al. 2006), this may be a reflection of the distinct lack of sampling efforts at the greatest hadal depths: For both historical and technological reasons, most studies have concentrated on the abyssal-hadal boundary. For example, recent studies using baited imaging technology have shown that very conspicuous, large decapod crustaceans that were previously thought to be absent from the hadal zone are indeed present (Jamieson et al. 2009b). Furthermore, trawling is an intrusive sampling method that generates noise and turbulence, and many mobile organisms, fishes in particular, will undoubtedly

detect and evade capture attempts. Indeed, the effectiveness of trawling, particularly at hadal depths, is hard to evaluate (Kullenberg 1951). Therefore, the reports of large numbers of fish observed from the *Archimède* (Pérès 1965) may well be plausible.

### New observations of hadal fish

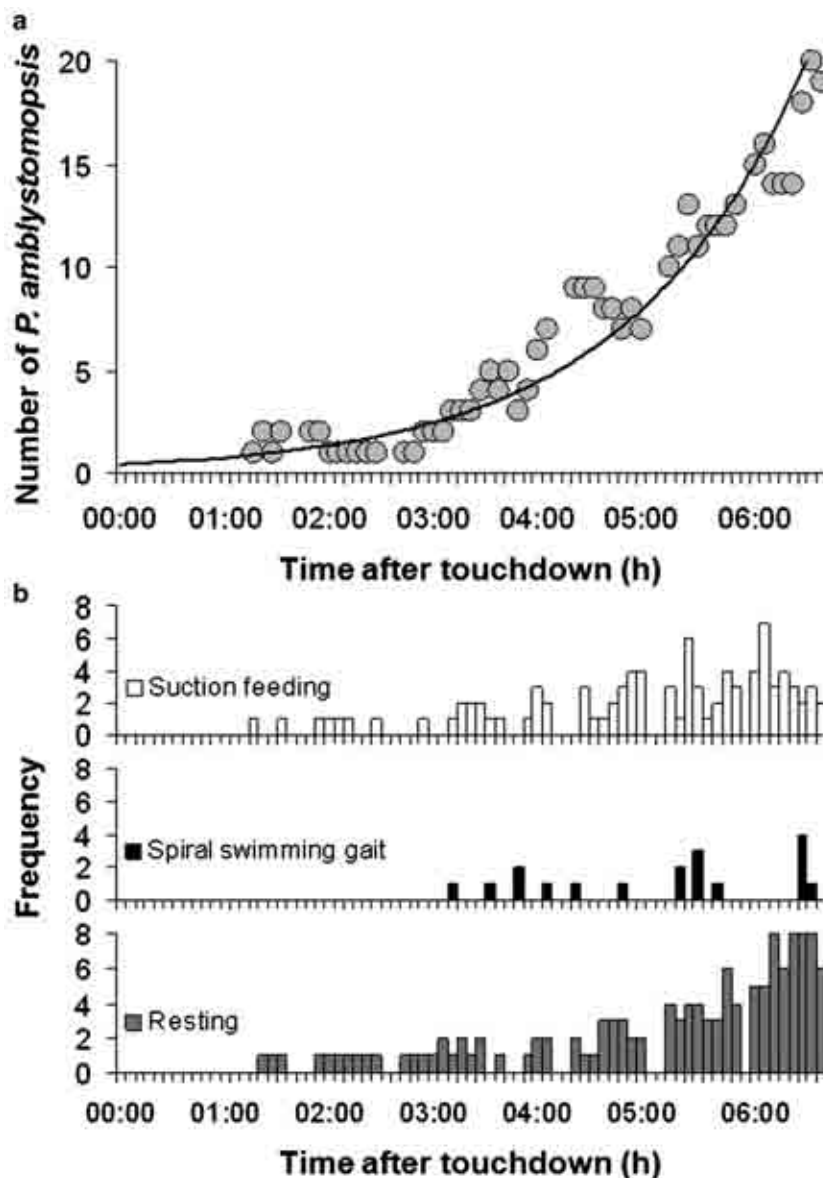
Recent *in situ* observations of hadal fauna captured by baited video camera from 7703 m in the Japan Trench (northwestern Pacific Ocean) reveal aggregations of hadal fish that suggest assessments of fish stocks using data obtained from historical trawls alone are unlikely to be representative of natural populations.

A free-fall baited lander, *Hadal-Lander A* (Jamieson et al. 2009a, 2009b), equipped with a time-lapse video camera, was deployed in the Japan Trench at 7703 m (36° 14.8'N 142° 49.7'E; 30 September 2008) from the Japanese research vessel *Hakuho-Maru*. The lander descended to the seafloor and remained static for about 6.5 hours until recalled to the surface by the jettisoning of its ballast weights. Equipped with a 3CCD video camera (HV-D30; Hitachi, Japan) positioned 1.0 m above the seafloor, looking down vertically at bait (approximately 0.5 kilograms of mackerel, *Scomber japonicus*), the lander was preprogrammed to record one minute of video footage in MPEG2 format at five-minute intervals. The field of view (68 centimeters [cm] × 51 cm = 0.35 square meter) was illuminated by two 50-watt lamps. The video was controlled and recorded autonomously, powered by a 24-volt lead-acid battery (Seabattery; DSP&L, United States). Salinity, pressure, and temperature were recorded using a SeaCat-19PlusV2 (Seabird Electronics, United States). Three cylindrical baited funnel traps (one large, 30 cm Ø × 40 cm; and two small, 10 cm Ø × 30 cm) were attached to the feet of the lander in order to collect benthic scavenging fauna (e.g., amphipod crustaceans, fish) for confirmation of species identifications made from video. Each one-minute video sequence was analyzed manually, frame by frame (25 frames per second). We estimated fish body lengths using a reference scale bar, adjusted to be level with the seafloor, positioned at the bottom of the field of view. We digitally analyzed only sequences where fish individuals were close to or in contact with the seafloor using proprietary software (ImageJ 1.42q, National Institutes of Health, United States), calibrated against the scale bar to minimize perspective error. Similarly, we estimated current velocity from video by tracking sediment particles resuspended by biological activity that were drifting close to the sediment-water interface. Pressure was converted to depth following Saunders (1981).

A total of 77 one-minute sequences were obtained over 6 hours and 40 minutes on the seafloor. Salinity and temperature were 34.68 and 1.9 degrees Celsius, respectively, over the observation period, and current velocity was estimated as between 2 and 4 cm per second. Pressure was recorded at 7901 decibars, which corresponds to a depth of 7703 m (Saunders 1981).

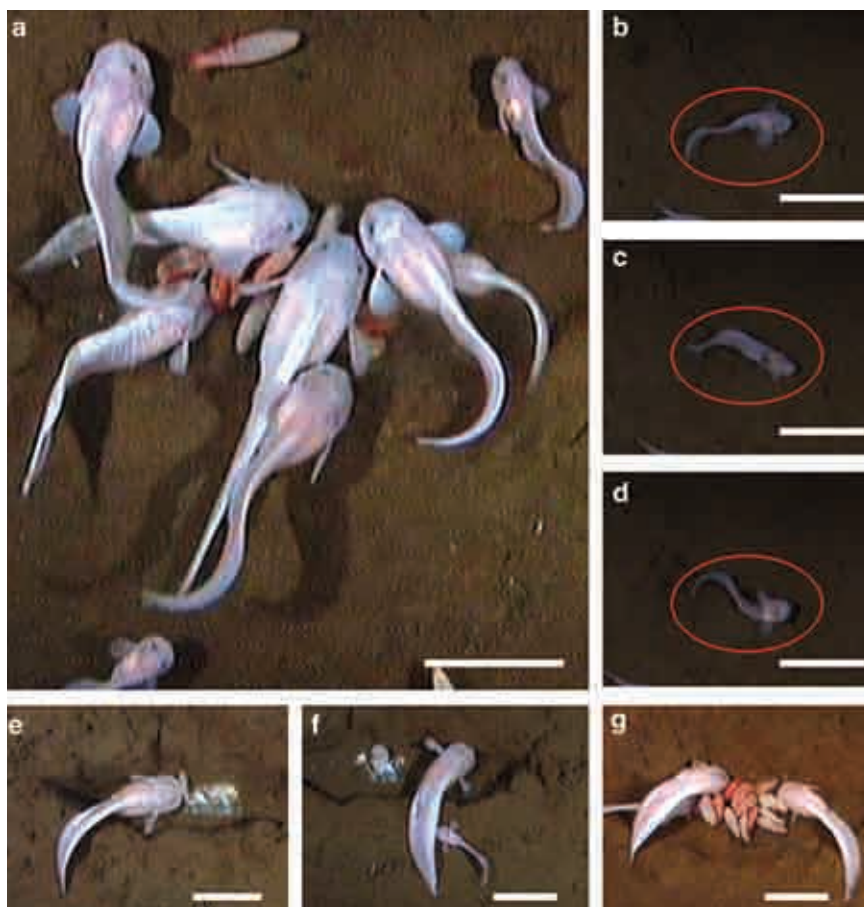
The first fish to arrive at the bait was a liparid, *Pseudoliparis amblystomopsis*, at 1 hour and 15 minutes after touchdown. The maximum abundance of fish observed within each one-minute video sequence increased exponentially during the following 5 hours, reaching a maximum of 20 at the end of recording (figure 1a; 6 hours 35 minutes). Adult liparids and juveniles aggregated together (figure 2a), and among the liparid individuals imaged, the maximum and minimum total body lengths were estimated as 30.0 cm and 7.4 cm, respectively. In one video sequence, it was possible to measure the lengths of 10 individuals with confidence without measuring the same fish twice, as they remained continuously in the field of view, providing an estimated mean body length of 19.8 cm ( $\pm 5.2$  standard deviations,  $n = 10$ ).

Most individuals approached the bait from down-current (as indicated by sediment disturbance). Some oriented themselves with their snouts directly over the bait, maintaining the same direction (figure 2a), whereas others slowly drifted out of view cross-current before returning to the bait moments later. The bait, which was partially embedded in the sediment, attracted numerous large amphipods (*Eurythenes* sp., 7.0 to 13.0 cm long) almost continuously for the period following two hours after touchdown (figure 2g). None of the liparids attempted to feed directly on the bait itself, but many were observed suction feeding on the small amphipods ( $< 2.0$  cm) that were attracted to the bait (figure 1b). On several occasions, a large individual was seen sucking sediment from the seafloor into the buccal cavity and ejecting it through the gills. Analysis of the time-lapse sequence (figure 1b) suggests that approximately 25% of the individuals within an aggregation exhibited suction-feeding behavior in the vicinity of the bait. Large amphipods were occasionally observed interfering with the tails or bodies of fish individuals, but such physical interference was thwarted by sudden and repeated body flicks. In addition, some fish individuals repeatedly flicked their heads and bodies against the seafloor, which at times turned them upside-down, allowing them to swim forward in a spiral configuration (figure 1b) while remaining in contact with the sediment surface (figure 2b, 2c, 2d). On average, 5% of individuals demonstrated this behavior (figure 1b), which often resulted



**Figure 1.** (a) The time course post touchdown (in hours) of the number of liparid *Pseudoliparis amblystomopsis* observed at 7703 meters in the Japan Trench. An exponential rise (fitted line:  $y = 0.4061e^{0.0531 \cdot 0.2x}$ ;  $x = \text{minutes}$ ;  $r^2 = 0.89$ ) in abundance occurs following first arrival after 1 hour and 18 minutes, reaching a maximum of 20 individuals after 6 hours and 35 minutes. (b) The time course after touchdown (in hours) of the count of individual *P. amblystomopsis* that exhibited suction feeding, spiral swimming gait, and resting.

in the adhesion of sediment to various parts of their bodies. In contrast, some individuals remained stationary and rolled onto one side if pushed by the current or other individuals (figure 2e, 2f, 2g). This stationary behavior was seen episodically even among several individuals that were otherwise very active. On average, 36% of individuals displayed such inactivity during observation (figure 1b), but we observed no specific events that may have led to the initiation or cessation of this behavior.



**Figure 2.** Images of liparid *Pseudoliparis amblystomopsis* at 7703 m in the Japan Trench taken from the baited video lander. (a) View of an aggregation of *P. amblystomopsis* at bait 5 hours and 30 minutes after touchdown. (b–d) Sequence of images 1.0 second apart showing a spiral swimming pattern of a small individual of *P. amblystomopsis* with the (b) dorsal, (c) flank, and (d) ventral sides of the fish in view (indicated in the red circle). (e–g) Typical postures when individuals were not actively feeding or swimming and presumed to be resting. In panel (g), the bait was covered by individuals of large amphipods, including *Eurythenes* species, sandwiched between two stationary individuals of *P. amblystomopsis*. All scale bars are 10 centimeters.

### Comparisons with bathyscaphe observations

The fish behaviors described above and those of other benthic megafauna are very similar to observations made by Pérès (1965), who descended in the bathyscaphe *Archimède* to 7300 m in the Puerto Rico Trench and completed a one-mile (1.6-kilometer) visual transect of the seafloor. According to the report, the benthic community was composed mostly of malacostracan (soft-shelled) crustaceans and fish. The most conspicuous crustaceans were a red shrimp about 10 to 12 cm long and two other less-frequently observed natantian decapods. Pérès also observed an isopod from the Asselota suborder, 7 to 8 cm long and 1 cm wide, with a rectangular body and ivory color. The isopod appeared to swim awkwardly while aided by the beating of its pleon. The fishes, believed to be a liparid species of the genus *Careproctus*, were much more numerous than crustaceans, and 200

individual fish were reported from the transect survey. The fish were mostly 10 to 12 cm long; a few were up to 25 cm in length. Whether these represented two related species or juveniles and adults of the same species could not be determined. The report describes that all had distinct black eyes and were generally pale pink in color, becoming darker with increasing body size. They were described as swimming “spirally” and often discontinuously, and some fish were observed to “fall” to the bottom, where they remained stationary for several minutes, always with their bodies slightly arched in a seemingly unbalanced position, typically lying on one side. Pérès (1965) also observed two individual fish, each with a slender gray-black body mixed with pink, similar to a zoarcid. The second species was thought to be a macrourid, approximately 30 cm long; however, no other details were noted.

Our recent observations from baited cameras in the Kermadec and the northern Japan trenches at depths of around 7000 m (Jamieson et al. 2009a, 2009b), as well as those presented here from 7703 m in the southern Japan Trench, are consistent with the observations of Pérès (1965). Red shrimps (*Benthescymus crenatus* and *Acanthephyra* sp.) have been observed at equivalent depths in both trenches, and in the Japan Trench, isopods of equal size, color, and description, which also appeared to swim awkwardly, have been noted (*Storothyngura* sp). Although no zoarcids have been recorded at hadal

depths, Jamieson and colleagues (2009a) reported two individuals of abyssal macrourid (*Coryphaenoides yaquinae*, 36 and 49 cm long) at depths of about 7000 m, which provides anecdotal credence to the observation made by Pérès (1965). The most startling similarity between the studies, however, is the description of the liparids. The liparids described here and by Jamieson and colleagues (2009a), *Pseudoliparis amblystomopsis* (formerly, *Careproctus*), are of similar size, color, and morphology to those documented during the *Archimède* dive. Furthermore, Pérès’s observations of individual fish swimming in an irregular spiral pattern as well as temporarily resting on the bottom in an unbalanced arched position mirror the behaviors we observed in liparids, including *Noto-liparis kermadecensis* from the Kermadec Trench. Spiral

swimming has also been described as “scratching” in shallower-water liparids; the behavior may be an attempt to remove parasites (e.g., parasitic copepods; Stein et al. 2006). Given the large number of amphipods attracted to the bait, it is possible that the behavior we observed is a response to amphipod encounters. With respect to the resting behavior, specimens captured in our funnel traps confirm that *P. amblystomopsis* has a distinctive ventral sucking disk. In other genera of liparids, such as *Careproctus*, researchers have reported observing the sucking disks being used as a means of attachment to the body of lithodid crabs for possible reproductive commensalism or parasitism in the shallower environments (Somerton and Donaldson 1998, Yau et al. 2000, Stein et al. 2006). Such behavior suggests that the bouts of resting behavior observed here may not be unusual, although most of the resting poses occurred on the surface of the soft sediment for *P. amblystomopsis* in the Japan Trench, and, in the case of *N. kermadecensis*, resting on the seafloor occurred even in the presence of relatively strong currents (of approximately 8 to 14 cm per second) in the Kermadec Trench (Jamieson et al. 2009a). When combined with the observations of Pérès (1965), and perhaps those of Stein and colleagues (2006), our observations of resting behavior may point to a response to unnatural perturbation. In the absence of any known predator, and together with the fishes’ characteristic low muscle mass, any excessive swimming in response to the presence of underwater vehicles may result in the fish rapidly becoming exhausted, necessitating temporary resting periods and precluding the initiation of active aggression or the fast-start escape responses known in shallower-occurring deep-sea fish (Bailey et al. 2003).

For the occurrence of hadal liparids, it is also important to consider the geographical location of the observations made by Jamieson and colleagues (2009a, 2009b), those presented here, and those of Pérès (1965). The *Archimède* dive was in the Puerto Rico Trench (west Atlantic), whereas the others were in the Japan Trench (northwestern Pacific), some 7000 nautical miles away and in a different ocean. Of all the known hadal liparids, none have been documented from the Puerto Rico Trench, but among the comparatively well-studied trenches in the Pacific, each appears to have an endemic species of liparid (Andriashev 1955, Nielsen 1964, Horikoshi et al. 1990, Andriashev and Pitruk 1993, Stein 2005, Jamieson et al. 2009a), suggesting that the liparid observed by Pérès (1965) may well be a hitherto undescribed new species. These combined observations suggest that liparid populations in the upper trench may diverge from those previously estimated from trawl data alone, although the behavior of these liparids in the presence of underwater vehicles has yet to be examined: Shallower-water liparids are known to exhibit species-specific responses to underwater vehicles (Stein et al. 2006). Further, although trawl sampling may yield low catch rates compared with nondestructive sampling

methods (such as baited camera systems), it is still important to address the issue of population patchiness. In the Japan Trench, Jamieson and colleagues (2009a) observed a single *P. amblystomopsis* at 6945 m, yet an aggregation of 20 individuals has been observed further south at 7703 m. Horikoshi and colleagues (1990) caught a single *P. amblystomopsis* from a trawl between 7420 and 7450 m in the southern Japan Trench, but later caught eight at the same depth in the north. In this study, the number of the liparid individuals increased exponentially in response to the landing of the baited camera, and such nonlinearity in arrival rates indicates evidence of patchy distribution or social organization of this species. Liparids are often characterized by low to very low fecundity and the possession of correspondingly large eggs (Mead et al. 1964, Stein 1980, Chernova et al. 2004). Such traits may indicate direct development of juveniles with probable involvement of parental care, which may in turn explain the observation of fish aggregation and their size ranges observed in this study. Furthermore, liparid species recorded in the hadal depths exhibit very limited bathymetric range of occurrence (stenobathic) in comparison with other characteristic deep-sea fish families such as macrourids and ophidiids (Jamieson et al. 2009a). Although an apparent patchy distribution could therefore be an artifact caused by sparse sampling across the limited bathymetric range, the spatial pattern of carbon flux and resulting variability in local food availability within trench systems may still play a part in explaining the local abundance of hadal liparid species. Rather than an effect of depth, apparent patchiness in fish abundance within a trench may be a reflection of resource availability and the ability of individual fish to respond to resource heterogeneity over time (seasonality) or space.

### Reappraisal of hadal fish records

It is clear that the current understanding of hadal fish population structure is woefully inadequate, giving impetus for the reanalysis of hadal fish records and the reappraisal of archived data regarding the occurrence and diversity of hadal species. The archival data used in the reappraisal were therefore extracted from global data sets accessed through FishBase (available from [www.fishbase.org](http://www.fishbase.org); Froese and Pauly 2009). Although the data set of fishes (Froese and Pauly 2009) has documented 15 species belonging to 6 families (3 Bathylagidae [deep-sea smelts], 1 Eurypharyngidae [gulpers], 1 Macrouridae [grenadiers], 1 Carapidae [pearlfish], 5 Ophidiidae [cusk-eels] and 4 Liparidae [snailfish]) described as occurring at hadal depths, a thorough examination of the original references reveals that many of these records are either erroneous or, at best, ambiguous (table 1).

The bathylagid *Lipolagus ochotensis* Schmidt 1938 (the eared blacksmelt) is a well-known mesopelagic fish that migrates vertically from deep (approximately 1000 m) to shallow waters (about 500 m) to feed at night (Radchenko 2007). Similarly, *Bathylagus pacificus* Gilbert 1890 (slender

**Table 1. Current list of fish species recorded at depths greater than 6000 meters. The reappraisal of each species' hadal status was made on the basis of further investigation of records and interpretation of available information. Depth ranges and their authority are collated from FishBase (Froese and Pauly 2009) with additional records presented in brackets.**

Species	Depth (m)	Authority [additional record]	Trench	Ocean	Hadal status
<b>Bathylagidae (deep-sea smelts)</b>					
<i>Lipolagus ochotensis</i>	0–6100	Schmidt 1938	Not specified	N Pacific	No, pelagic
<i>Pseudobathylagus milleri</i>	0–6600	Jordan and Gilbert 1898	Not specified	N Pacific	No, pelagic
<i>Bathylagus pacificus</i>	230–7700	Gilbert 1890	Japan	NW Pacific	No, pelagic
<b>Eurypharyngidae (gulpers)</b>					
<i>Eurypharynx pelecyanoides</i>	500–7625	Vaillant 1882	Not specified	E Pacific	No, pelagic
<b>Macrouridae (grenadiers)</b>					
<i>Coryphaenoides yaquinae</i>	3400–5800	Iwamoto and Stein 1974	(Abyssal)	NW Pacific	Yes, also abyssal
	[6160]	[Horibe 1982]	Japan	NW Pacific	
	[6945]	[Jamieson and colleagues 2009a]	Japan		
	[6380–6450]	[Endo and Okamura 1992]	Japan		
<b>Carapidae (pearlfish)</b>					
<i>Echiodon neotes</i>	8200–8300	Markle and Olney 1990	Kermadec	SW Pacific	Inconclusive
<b>Ophidiidae (cusk-eels)</b>					
<i>Bassozetus zenkevitchi</i>	0–6930	Rass 1955	Not specified	N Pacific	Inconclusive
<i>Leucicorus atlanticus</i>	4580–6800	Nielsen 1975	Cayman	W Atlantic	Yes, also abyssal
<i>Abyssobrotula galathea</i>	3110–8370	Nielsen 1977	Puerto Rico	W Atlantic	Yes (inconclusive), also abyssal
	[2330]	[Shcherbachev and Tsinovsky 1980]	Puerto Rico		
<i>Holcomycteronus profundissimus</i>	5600–7160	Roule 1913	Sunda	Indian	Yes, also abyssal
<i>Apagesoma edentatum</i>	5082–8082	Carter 1983	Not specified	W Atlantic	Inconclusive
<b>Liparidae (snailfish)</b>					
<i>Notoliparis antonbruuni</i>	6150	Stein 2005	Peru-Chile	SE Pacific	Yes, but rare
<i>Notoliparis kermadecensis</i>	6660–6770	Nielsen 1964	Kermadec	SW Pacific	Yes, endemic
	[6890]	[Jamieson and colleagues 2009a]	Kermadec		
<i>Pseudoliparis amblystomopsis</i>	7210–7230	Andriashev 1955	Kurile-Kamchatka	NW Pacific	Yes, endemic
	[7420–7450]	[Horikoshi and colleagues 1990]	Japan	NW Pacific	
	[6945]	[Jamieson and colleagues 2009a]	Japan		
	[7703]	[present contribution]	Japan		
<i>Pseudoliparis belyaevi</i>	7565–7587	Andriashev and Pitruk 1993	Japan	NW Pacific	Yes, but rare

blacksmelt) and *Pseudobathylagus milleri* (Jordan and Gilbert 1898; stout blacksmelt) are also mesopelagic; these bathylagids are common in the Bering Sea, the Sea of Okhotsk, and the northwestern Pacific Ocean, and therefore occupy the pelagic waters overlying the Aleutian, Kuril-Kamchatka, and Japan trenches. Bathylagid larvae are also known to occur seasonally in the surface waters (< 300 m) of the northwestern Pacific (Sassa and Kawaguchi 2006, Sassa et al. 2007). For relatively well-studied fishes that are known to rely heavily on the mesopelagic and epipelagic zones for feeding and spawning, a range of depth greater than 6000 m is clearly unlikely. Given that they are relatively small (mean body length = 16, 25, and 16.5 cm, respectively) and occur in the pelagic zones overlying hadal trenches, it seems more likely that these records reflect incidental catches during trawl hauling to the surface.

*Eurypharynx pelecanoides* Vaillant 1882 (gulper eel) is another well-known bathypelagic fish (Gartner 1983, Inoue et al. 2003), with a problematic maximum recorded depth of 7625 m (Coad and Reist 2004). Generally, this fish is found between 1000 and 3000 m above the seafloor (Owre and Bayer 1970) at depths between 1200 and 1400 m (Masuda et al. 1984). One report of urchin fragments found in a specimen's stomach (suggesting bottom feeding; Marshall 1954) was briefly acknowledged, but later dismissed (Gartner 1983). The origins of the 7625-m samples are unclear, but the available biological background of this species suggests that it is unlikely that *E. pelecanoides* occurs at hadal depths.

Macrourids are a diverse, well known, and abundant family of deep-sea gadiform fishes (Wilson and Waples 1983). *Coryphaenoides yaquinae* Iwamoto and Stein 1974, the deepest-living macrourid, is restricted to the Pacific Ocean and is well documented down to 5900 m (Priode and Smith 1986, Armstrong et al. 1991). Although primarily a deep-abyssal scavenger, it has also been observed *in situ* at 6160 m (Horibe 1982) and 6945 m (Jamieson et al. 2009a) in the Japan Trench, thus transcending the abyssal-hadal boundary. The most ubiquitous deep macrourid in the Atlantic is *Coryphaenoides armatus* Hector 1875, a species with a maximum known depth of 5180 m (Cohen et al. 1990). Interestingly, Pérès (1965) observed a macrourid at about 7300 m deep in the Puerto Rico Trench in the Atlantic Ocean; if this identification was indeed correct, then it means that *C. armatus* lives about 2000 m deeper than previously thought, that *C. yaquinae* does occur in the Atlantic, or there is another species of macrourid—possibly a new and undescribed species—in the deep Atlantic Ocean.

The genus *Echiodon* Thompson 1837 comprises a group of 12 known species of pearlfishes (family Carapidae) with a known depth range of between 1800 and 2000 m (Markle and Olney 1990, Williams and Machida 1992) with the sole exception of *Echiodon neotes* Markle and Olney 1990. It is known from a single catch made between 8200 and 8300 m in the Kermadec Trench. It is recorded as being demersal, but is debatably pelagic (Nielsen et al. 1999). Although its

presence at hadal depths remains unresolved, it is highly questionable that a single species from this genus would be found about 6300 m deeper than any other previously documented *Echiodon* specimen.

There are records of five ophidiids with a depth range exceeding 6000 m: *Bassozetus zenkevitchi* Rass 1955, *Leucicorus atlanticus* Nielsen 1975, *Holcomycteronus profundissimus* (Roule 1913), *Apagesoma edentatum* Carter 1983 and *Abyssobrotula galathea* Nielsen 1977, all of which are relatively rare.

*Bassozetus zenkevitchi* is unique among species of *Bassozetus* in that it is pelagic, although benthic captures have been acknowledged (Nielsen and Merrett 2000). The recorded but abnormally large depth range of 0 to 6930 m presented in the archival data is very misleading, stemming from a conical fishing net hauled vertically from 6930 m to the surface during the RV *Vityaz* expedition in 1957. Vertical fishing nets do not permit an exact depth of capture to be ascertained, hence the entire catch is labeled between 0 and 6930 m, regardless of where in the water column the species were captured. Furthermore, the fine condition of all specimens captured by these gears strongly suggested that *B. zenkevitchi* occur pelagically (Machida and Tachibana 1986, Nielsen and Merrett 2000) rather than demersally at the hadal seafloor. The distribution of *B. zenkevitchi* is concentrated in the vicinity of the Kuril-Kamchatka, Japan, and Izu-Bonin trenches, with a few specimens from the mid-Pacific and Bering Sea (Orr et al. 2005). As *B. zenkevitchi* may well occur abyssopelagically, its hadal status seems unlikely.

*Leucicorus atlanticus* was once considered a unique hadal fish species of the Caribbean region (Rass et al. 1975), but it is now known to reside in lower abyssal to hadal depths (4590 to 6845 m; Anderson et al. 1985). It is demersal, and repeated catches in the Cayman Trench give no reason to doubt its hadal occurrence. *Holcomycteronus profundissimus* (Roule 1913), formerly *Bassogigas* (Nielsen 1964), is geographically ubiquitous; distributed in the Atlantic, Pacific, and Indian oceans; and has a known depth range of 5600 to 7160 m (Nielsen et al. 1999). Its hadal records are from the Sunda (Java) Trench and the Moseley Trench, and these records appear to be accurate.

The ophidiid *Apagesoma edentatum* is a rare species with a recorded range of 5082 to 8082 m in the archived data, but descriptions by Anderson and colleagues (1985) and later by Nielsen and colleagues (1999) place its range between 2560 and 5082 m. The origins of the 8082-m entry are unclear. *Apagesoma edentatum* is thought to be demersal, and its stomach contents suggest that it is a scavenger (Carter 1983), but its recorded presence at hadal depths is most likely a result of reporting error.

The ophidiid *Abyssobrotula galathea* is currently claimed as the deepest vertebrate ever found (8370 m in the Puerto Rico Trench; Nielsen 1977). Of the 17 records available, 1 is from bathyal depths (2330 m; Shcherbachev and

Tsinovsky 1980), 14 are from abyssal depths, and 2 are from hadal depths (between 3100 and 8370 m; Machida 1989). Although the deeper records for *A. galathea* are from close to or inside the Puerto Rico, Japan, and Izu-Bonin trenches (Machida 1989), the specimens were obtained using a nonclosing trawl net. Nielsen (1964) and Nielsen and Munk (1964) questioned whether the recovered individuals were of pelagic or demersal origin, as 15 genera of pelagic fish were reported from the same trawl. On the basis of stomach contents, *A. galathea* could feasibly be thought to originate from the bottom. Indeed, when Shcherbachev and Tsinovsky (1980) reported on (by then) a total of 12 finds (all bathyal or abyssal), they stated that one fish had been caught in a pelagic trawl 400 to 800 m above the bottom. Given the high incidence of occurrences from abyssal depths and the use of a nonclosing trawl net, the true depth range of this species remains unresolved. Without further discussion, however, the fish has been deemed demersal and is assumed to occur down to 8370-m depths.

The liparids *Notoliparis antonbruuni* Stein 2005 and *Pseudoliparis belyaevi* Andriashev and Pitruk 1993 are extremely rare; the former is known from only one very poor specimen caught at 6150 m off the coast of Peru (Stein 2005), and the latter from a specimen caught between 6380 and 7587 m in the Japan Trench (Chernova et al. 2004). Although there is no reason to doubt a hadal occurrence of these species, further sampling might indicate they are more widespread than the location of the type specimen would suggest. Although similarly rare (it has been trawled only once), *Notoliparis kermadecensis* was recently filmed *in situ* at 6890 m, confirming its hadal status (Jamieson et al. 2009a). *Pseudoliparis amblystomopsis* is perhaps the most commonly found hadal fish species, with several trawl records (Horikoshi et al. 1990, Chernova et al. 2004) and *in situ* observations (Jamieson et al. 2009a, this contribution).

## Conclusion

We have been unable to find unequivocal evidence that fish reach full ocean depths, or indeed inhabit depths beyond the current, although controversial, deepest record held by *A. galathea* (8370 m; Nielsen 1977). Disputes over the true depths of known hadal specimens captured by trawling are unlikely to be resolved, as these records lack unequivocal proof of demersal origin. On the basis of the reappraisal of archival data, however, it appears that there are fewer known species of hadal fish than current opinion would reflect. The three bathylagids, the eurypharyngid, and the carapid appear to be incidental pelagic catches. Although it is feasible that the ophiidiid *B. zenkevitchi* could be hadal, vertical trawling does not offer any means of confirming the depth of capture, and furthermore produces a misleadingly large depth range. In the case of *A. edentatum*, it appears likely that the depth entry is an error. The potential to find more ophiidiids

at hadal depths is, however, more likely, especially given that there are many species known from greater than 5000-m depths. The liparids are also the only group that has been repeatedly sampled from multiple trenches at hadal depths, allowing the generality of any trends to be continually revised and defined. Although two species (*N. antonbruuni* and *P. belyaevi*) are known from single captures, *N. kermadecensis* and *P. amblystomopsis* appear to be endemic to the Kermadec Trench and Japan/Kuril-Kamchatka Trench, respectively. *Careproctus sandwichensis* is known only from the South Sandwich Trench in the Southern Ocean (Andriashev and Stein 1998), and the *Careproctus* species observed by Pérès (1965) in the Puerto Rico Trench potentially offers another endemic liparid. Notwithstanding errors in interpretation due to differences in sampling effort, the liparids do appear to dominate and characterize hadal fish fauna.

A consistent feature across the hadal literature is that the return of ecological information is highly dependent on the methodology used. While destructive sampling such as trawling allows unambiguous identification, genetic analysis, and examination of physiology and stomach contents, nondestructive methods, such as the *Archimède* bathyscaphe and baited camera systems, allow the determination of extended observations of environment-species relations and intra- and interspecific interactions within a hadal context. Evidence from the latter casts doubt on current conceptions of hadal structure and the roles of hadal fish in ecological interactions, suggesting that hadal communities are not as simple as have been assumed. The fact that 20 liparids can aggregate at bait in only six hours at 600 m shallower than the maximum known depth of fish, combined with the variability in hadal fish occurrences recorded to date, suggests that fish may well occur at far deeper depths than previously thought. It is clear that our current understanding of the hadal environment is inadequate; this presents an immediate challenge for ecologists to understand the contribution of hadal communities to deep ocean functioning, to grasp the extent to which these systems are connected to shallower environments, and to establish how such communities will be affected by global change.

## Acknowledgments

We thank Asako K. Matsumoto, Kumiko Kita-Tsukamoto, Hidekazu Tokuyama, and Mutsumi Nishida at the Ocean Research Institute, University of Tokyo, Japan, and the crew and company of the *Hakuho-Maru* KH-08-03. We acknowledge Laura Burns and Debbie Crockard (University of Aberdeen) for their assistance at sea, and Owen Gaffney at Planet Earth Online (<http://planetearth.nerc.ac.uk/>) and Rebecca Morrelle at the BBC for formulating our outreach program. This work, part of the HADEEP project, was supported by the Natural Environmental Research Council (United Kingdom) and the Nippon Foundation (Japan).

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