

Invertebrate population genetics across Earth's largest habitat: The deep-sea floor

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Abstract

Despite the deep sea being the largest habitat on Earth, there are just 77 population genetic studies of invertebrates (115 species) inhabiting non-chemosynthetic ecosystems on the deep-sea floor (below 200 m depth). We review and synthesize the results of these papers. Studies reveal levels of genetic diversity comparable to shallow-water species. Generally, populations at similar depths were well connected over 100s–1,000s km, but studies that sampled across depth ranges reveal population structure at much smaller scales (100s–1,000s m) consistent with isolation by adaptation across environmental gradients, or the existence of physical barriers to connectivity with depth. Few studies were ocean-wide (under 4%), and 48% were Atlantic-focused. There is strong emphasis on megafauna and commercial species with research into meiofauna, “ecosystem engineers” and other ecologically important species lacking. Only nine papers account for ~50% of the planet's surface (depths below 3,500 m). Just two species were studied below 5,000 m, a quarter of Earth's seafloor. Most studies used single-locus mitochondrial genes revealing a common pattern of non-neutrality, consistent with demographic instability or selective sweeps; similar to deep-sea hydrothermal vent fauna. The absence of a clear difference between vent and non-vent could signify that demographic instability is common in the deep sea, or that selective sweeps render single-locus mitochondrial studies demographically uninformative. The number of population genetics studies to date is miniscule in relation to the size of the deep sea. The paucity of studies constrains meta-analyses where broad inferences about deep-sea ecology could be made.

KEYWORDS

benthic, deep sea, genetic connectivity, marine, population genomics, vulnerable marine ecosystems

1 | INTRODUCTION

The deep-sea floor is widely regarded as the largest ecosystem on Earth (Webb, Vanden Berghe, & O'Dor, 2010), covering around 65% of the planet's surface (Danovaro et al., 2008). Despite its remoteness to the lives of humans, it is now understood that the deep sea provides a range of important ecosystem functions, goods and

services, such as global biogeochemical cycling, carbon sequestration, the provision of food biomass (fisheries), bioprospecting potential, and vast energy and mineral reserves (Thurber et al., 2014). With the accumulation of anthropogenic waste (Thiel, 2003), including recently discovered microplastics (Van Cauwenberghe, Vanreusel, Mees, & Janssen, 2013), the seemingly inexorable increase in biomass harvesting (Norse et al., 2012), and huge areas of the seabed

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under signed exploration contracts (~1,843,350 km²; Hein, Mizell, Koschinsky, & Conrad, 2013), there is a growing awareness that the ecosystems and resources in the deep sea need to be responsibly and sustainably managed (Mengerink et al., 2014).

Basic ecological information (e.g., species ranges, population subdivision, population genetic diversity, dispersal capability and demographic parameters) is lacking for all but a few species (Mengerink et al., 2014). This knowledge is essential for the delineation of conservation units (Fraser & Bernatchez, 2001) and the design of marine-protected areas (Wedding et al., 2013) to maintain biodiversity—a proxy for ecosystem functioning (Danovaro et al., 2008). This data deficit reflects the extreme remoteness of the deep sea compared with many shallow-water or terrestrial environments; hampering efforts to elucidate broad patterns of biodiversity and ecosystem function in the deep sea (McClain & Schlacher, 2015). In an environment where traditional ecological data collection methods are extremely difficult, population genetics, that is, the comparison of genetic diversity within and between populations of individuals, allows deep-sea ecologists to model patterns of connectivity and genetic diversity; gaining insights into the dynamics and resilience of deep-sea populations.

Up to now, however, there has been a noticeable skew in deep-sea invertebrate population genetic research effort towards chemosynthetic environments, despite chemoautotrophic production accounting for roughly 10% of the total organic carbon flux to the deep sea (Levin, Baco, et al., 2016). Chemosynthetic ecosystems have generated great interest within the wider scientific community (Van Dover, German, Speer, Parson, & Vrijenhoek, 2002) as has their utility as natural one-dimensional stepping-stone models for investigating metapopulation dynamics (Vrijenhoek, 2010). However, the ephemerality and resultant perpetual non-equilibrium (migration–drift) conditions characteristic of vent habitats (Jollivet, Chevallon, & Planque, 1999) could limit the relevance of such studies to the wider deep sea, as other deep-sea habitats may be long-lived and relatively stable, for example, deep-water coral (Schröder-Ritzrau, Freiwald, & Mangini, 2005), or vast and continuous, such as the sediment-covered abyssal plains.

The last large-scale review of deep-sea population genetics was almost two decades ago (Creasey & Rogers, 1999). The aim of this study is to augment that previous work, focusing more narrowly on population genetic studies for deep-sea benthic invertebrates that are *not* endemic to, or strongly associated with, chemosynthetic ecosystems (e.g., hydrothermal vents, hydrocarbon seeps, and wood and whale falls). We bring together information from every publication available to present a historical narrative of the subject as well a critical appraisal of the prevailing paradigms relevant to the deep sea. In addition to integrating these studies into a broad research narrative spanning nearly half a century of research, this review aims to evaluate and assess the way that these studies have shaped our understanding of deep-sea benthic communities in general, and have provided information useful for the stewardship of the deep sea. Summary tables and figures are used to reveal and prompt discussion of research effort biases of geographical and taxonomic scope, depth range and habitat type,

as well as highlighting limitations in sampling, and suggestions of future best practices. In addition, the impact of changes in the use of prevailing genetic techniques and bioinformatic tools is discussed, with emphasis on the promise heralded by high-throughput next-generation sequencing (NGS) techniques in spurring further research in this field.

Henceforth, for the purpose of brevity, when mentioning deep-sea population genetics, we refer to research on non-chemosynthetic benthic invertebrate species. For clarity, we define the deep sea as below 200 m depth, which, with the exception of Antarctica, generally excludes continental shelf communities (Gage & Tyler, 1991).

2 | METHODS

We undertook a thorough search of published literature using a variety of key words such as “population genetics,” “population connectivity,” “population diversity,” “phylogeography,” “deep sea,” “population genomics.” Additional literature was found in the reference lists of papers. Studies were included herein if they explicitly investigated, statistically characterized, and discussed population genetic diversity and/or connectivity. We acknowledge that the boundary between population genetics, phylogeography, and phylogenetics is increasingly indistinct (Knowles, 2009). We have consequently chosen to exclude studies that featured multiple individuals of a species but only employed barcoding, phylogenetic tree-building, qualitative/descriptive methods, or clustering techniques (a non-exhaustive list is given in Supporting Information) as they often describe phylogeographical or taxonomic diversity, such as cryptic species, but do not explicitly investigate the dynamics of within- and between-population genetic diversity, for example, Glazier and Etter (2014). Conversely, we have included early studies which describe population genetic diversity (e.g., Gooch & Schopf, 1972) but have considered the data within the context of understanding the mechanisms governing the maintenance of genetic diversity. For a detailed discussion regarding the importance of considering species as hypotheses in population genetic connectivity studies, we refer you to Pante et al. (2015). Papers were excluded if we could not reasonably infer that samples were collected from below 200 m and the known species range was within shallower waters. Benthic invertebrate species collected from the seafloor, for example, trawl, epibenthic sledge or remotely operated vehicle, were included in our analyses. Species were included if they were considered not chemosynthetically associated, which for the purposes of review we consider as any that do not appear to be exclusive to, or derive the bulk of their nutrition from, reducing habitats. Thus, we included a study featuring the squat lobster *Munidopsis lauensis* sampled at vents, because it is also found in non-chemosynthetic habitats and cannot therefore be considered endemic, merely an opportunistic predator and scavenger (Thaler et al., 2014).

The resulting benthic deep-sea population genetics papers reviewed here are as comprehensive as possible and are listed in Table 1.

TABLE 1 Overview of deep-sea (>200 m depth) population genetics publications (in date order)

	Study organism(s)	Depth of populations	Geographical location	Details	a	b	References
1	Brittle star: <i>Ophiomusium lymani</i>	1,700–2,700 m	Off N. Carolina, USA	Alloz. elect. 1 locus, N = 233			Doyle (1972)
2	Sea urchin: <i>Gracilechinus affinis</i>	1,825–2,080 m	NW Atlantic and E Pacific	Alloz. elect. 4 loci, N = 3–7			Gooch and Schopf (1972)
	Sipunculid: Unknown sp.	1,825–2,070 m		4 loci, N = 3–7			
	Brittlestar: <i>O. lymani</i>	1,825–1,860 m		8 loci, N = 12			
	Shrimp: <i>Pandalopsis ampla</i>	1,238–1,257 m		15 loci, N = 8–13			
	Squat lobster: <i>Galacantha diomedea</i>	1,238–1,257 m		12 loci, N = 6			
	Armoured sea cucumber: <i>Psolus</i> sp.	2,050–2,070 m		9 loci, N = 11			
	Bivalves: <i>Jupiteria pontonia</i>	1,033–1,236 m		12 loci, N = 9–13			
	<i>Malletia</i> sp.	1,033–1,236 m		10 loci, N = 8			
3	Brittlestar: <i>O. lymani</i>	1,244 m	NE Pacific (San Diego trough)	Alloz. elect. 11 loci, N = 62–195			Ayala and Valentine (1974)
4	Sea stars: <i>Diplopteraster multipes</i>	15–1,170 m	NE Pacific (San Diego trough)	Alloz. elect. 5 loci, N = 3			Ayala et al. (1975)
	<i>Myxoderma sacculatum</i> ^c	200–1,000 m		6 loci, N = 4			
	<i>Nearchaster aciculosus</i>	300–2,100 m		17 loci, N = 17			
	<i>Pteraster jordani</i>	500–1,800 m		10 loci, N = 7			
5	Brachiopod: <i>Frieleia halli</i>	690–1,244 m	NE Pacific (San Diego trough)	Alloz. elect. 12 loci, N = 20–97			Valentine and Ayala (1975)
6	Sea stars: <i>Dytaster insignis</i>	2,580–2,780 m	NW Atlantic	Alloz. elect. 5 loci, N = 5–48			Murphy et al. (1976)
	<i>Psilaster andromeda</i> ^c <i>florae</i>	390–500 m		2 loci, N = 18			
	<i>Benthopecten simplex</i> ^c	2,580–2,626 m		5 loci, N = 4–30			
	<i>Zoroaster fulgens</i>	2,580–2,626 m		3 loci, N = 30			
	Brittle stars: <i>O. lymani</i>	1,328–1,986 m		6 loci, N = 43–86			
	<i>Ophiura</i> ^c <i>sarsii</i>	370–500 m		1 locus, N = 41			
	<i>Ophiophalma armigerum</i> ^c	2,745–2,780 m		2 loci, N = 12			
	<i>Ophiocten</i> ^c <i>gracilis</i> ^c	390–500 m		2 loci, N = 15			
7	Brittle stars: <i>Amphiophiura</i> ^c <i>bullata</i>	1,058 m	NE Atlantic	Alloz. elect. 13 loci, N = 25			Costa and Bisol (1978)
	<i>O. lymani</i>	1,900 m		9 loci, N = 47			
	Gastropod: <i>Buccinum</i> sp.	1,058 m		11 loci, N = 22			
	Crustacea: <i>Munidopsis hamata</i>	1,331 m		7 loci, N = 23			
8	Trochid gastropod: <i>Bathybembix bairdii</i>	579–1,156 m	California, E Pacific	Alloz. elect. 5 loci, N = 17–141			Siebenaller (1978)
9	Sea cucumber: <i>Benthogone rosea</i>	2,100 m	NE Atlantic and W Atlantic	Alloz. elect. 6 loci, N = 51			Bisol et al. (1984, as reported in Costa, Bisol, & Sibuet, 1982)
	<i>Benthoctes typica</i>	4,150 m		5 loci, N = 86			
10	Pink shrimp: <i>Pandalus borealis</i> ^d	171–315 m	Japan, N Pacific and Arctic	Alloz. elect. 4 loci, N = 61–482			Kartavtsev, Berenboim, and Zgurovsky (1991)
11	Pink shrimp: <i>P. borealis</i> ^d	Unknown	Japan, NW Pacific	Alloz. elect. 4 loci, N = 15–457			Kartavtsev, Zgurovsky, and Fedina (1993)
12	Pink shrimp: <i>P. borealis</i> ^d	171–315 m	Japan, N. Pacific, Arctic	Alloz. elect. 5 loci, N = 119–596			Kartavtsev (1994)
13	Red crab: <i>Chaceon quinquegens</i> ^d	860–1,042 m	Gulf of Mexico, Caribbean	Alloz. elect. 13 loci, N = 36–72			Diehl and Biesiot (1994)
14	Brittle star: <i>O. lymani</i>	1,708–2,500 m	NE Atlantic	Alloz. elect. 4 loci, N = 18–70			Hensley, Beardmore, and Tyler (1995)
15	Anemones: <i>Stephanauge</i> ^c <i>inornata</i>	1,000–2,350 m	NE Atlantic	Alloz. elect. 5 loci, N = 42–75			Bronsdon, Rogers, Tyler, Rice, and Gage (1997)
	<i>Sicyopus</i> ^c <i>commensalis</i>	4,505–4,877 m		7 loci, N = 55			

(Continues)

TABLE 1 (Continued)

	Study organism(s)	Depth of populations	Geographical location	Details	a	b	References
16	Spider crab: <i>Encephaloides armstrongi</i>	150–650 m	Oman	Alloz. elect. 5 loci, N = 18–203			Creasey, Rogers, Tyler, Young, and Gage (1997)
17	Shrimp: <i>P. borealis</i> ^d	Unknown	Arctic—Icelandic waters and Denmark Strait	Alloz. elect. 3 loci, N = 110–192			Jónsdóttir et al. (1998)
18	Protobranch bivalve: <i>Nucula</i> ^c <i>atacellana</i>	1,102–3,834 m	NW Atlantic	16S (196 bp) N = 4–17			Chase et al. (1998)
19	Shrimp: <i>Aristeus antennatus</i> ^d	Unknown	Mediterranean	Alloz. elect. 15 loci, N = 24–57			Sardà, Bas, Roldán, Pla, and Lleonart (1998)
20	Squat lobster: <i>Munidopsis scobina</i>	900–1,000 m	Oman, W Indian Ocean	Alloz. elect. 4 loci, N = 171–256			Creasey, Rogers, Tyler, Gage, and Jollivet (2000)
21	Shrimp: <i>P. borealis</i> ^d	116–680 m	NE Atlantic—Norwegian fjords, Barents Sea, Svalbard	Alloz. elect. 3 loci, N = 34–317			Drengstig et al. (2000)
22	Shrimp: <i>P. borealis</i> ^d	Unknown	NW Atlantic (NE Canada)	Alloz. elect. 8 loci, N = 12–263			Sévigny et al. (2000)
23	Gastropod: <i>Frigidoalvania brychia</i>	457–1,102 m	NW Atlantic	16S (136 bp) N = 10–16			Quattro, Chase, Rex, Greig, and Etter (2001)
24	Octopus: <i>Octopus vulgaris</i> ^d	250–400 m	Mediterranean	Alloz. elect. 13 loci, N = 20–30			Maltagliati et al. (2002)
25	Red crab: <i>C. quinquegens</i> ^d <i>Chaceon fenneri</i> ^d <i>Chaceon affinis</i> ^d	465–951 m 335 m Unknown	Cross-Atlantic: Gulf of Mexico, W to E Atlantic	16S (379 bp) N = 10–13 N = 11 N = 3			Weinberg et al. (2003)
26	Coral, reef building: <i>Lophelia pertusa</i>	200–1,000 m	NE Atlantic (UK, France and Norway)	ITS1 and ITS2 (834–1,004 bp) N = 2–21 10 microsats N = 2–165			Le Goff-Vitry, Pybus, and Rogers (2004) and Le Goff-Vitry and Rogers (2005)
27	Whelk: <i>Buccinum tsubai</i> ^d	300–1,104 m	Japan	16S (421 bp) N = 2–5			Iguchi et al. (2004)
28	Octocoral: <i>Corallium lauuense</i> ^c	385–535 m	Hawaii	3 microsats N = 1–32			Baco and Shank (2005)
29	Protobranch bivalves: <i>Ennucula</i> ^c <i>similis</i> <i>Nucula</i> ^c <i>atacellana</i> <i>Clencharia</i> ^c <i>abyssorum</i> <i>Ledella</i> <i>ultima</i>	1,102–3,912 m 1,102–3,912 m 1,102–3,912 m 1,102–3,912 m	NW Atlantic	16S rRNA mt (~200 bp) N = 5–10 N = 4–17 N = 2–19 N = 3–16			Etter et al. (2005)
30	Bivalve: <i>Nucula</i> ^c <i>atacellana</i>	1,102–3,912 m	Pan-Atlantic—18 localities in Argentina, N. America & W. EU basins	16S (~200 bp) N = 1–18			Zardus et al. (2006)
31	Shrimp: <i>P. borealis</i> ^d	150–550 m	Arctic	RAPD 34 loci, N = 19–31			Martinez et al. (2006)
32	Squat lobsters: <i>Munida thoe</i> <i>Munida zebra</i> <i>Munida acantha</i> <i>Eumunida annulosa</i> <i>Eumunida sternomaculata</i>	220–430 m 200–610 m 39–460 m 375–650 m 418–650 m	New Caledonia seamounts	COI (~600 bp) N = 1–4 N = 2–5 N = 1–8 N = 1–4 N = 1–5	X X X X X	X X X X X	Samadi, Botton, Macpherson, Forges, and Boisselier (2006)
	Gastropod: <i>Sassia remensa</i> <i>Nassaria problematica</i>	Unknown Unknown		N = 1–4 N = 4	X X	X X	

(Continues)

TABLE 1 (Continued)

	Study organism(s)	Depth of populations	Geographical location	Details	a	b	References
33	Crinoid: <i>Promachocrinus kerguelensis</i> (A)	116–315 m	Antarctic	COI (623 bp), CytB (663 bp) N = 1–7	X	X	Wilson et al. (2009)
34	Foraminifera <i>Epistominella exigua</i> <i>Cibicidoides^c wuellerstorfi</i> <i>Oridorsalis umbonatus</i>	572–4,975 m 572–4,975 m 572–4,975 m	Arctic and Antarctic	ITS (865–1,136 bp). N = 13–40 N = 53 N = 54			Pawlowski et al. (2007)
35	Whelks: <i>Buccinum tsubai^d</i> <i>Neptunea constricta^d</i>	300–1,104 m 229–766 m	Japan	COI (490 bp) N = 4–9 N = 1–4	X X	X X	Iguchi et al. (2007)
36	Brittle star: <i>Astrotoma agassizii</i>	96–900 m	S America to Antarctic Peninsula	16S (~500 bp), COI (550 bp) N = 1–18	X	X	Hunter and Halanych (2008)
37	Shrimp: <i>A. antennatus^d</i>	450–550 m	W & central Mediterranean	Mt control region (369 bp) N = 8–29	X	X	Maggio et al. (2009)
38	Shrimp: <i>A. antennatus^d</i>	Unknown	W Mediterranean	16S (547 bp), COI (514 bp) N = 36–59	X	X	Roldán et al. (2009)
39	Sea cucumber: <i>Doris kerguelensis</i>	24–520 m	Antarctica	COI (627 bp), 16S (484 bp) N = 1–100	X	X	Wilson et al. (2009)
40	Foraminifera: <i>Epistominella exigua</i>	1,905–1,990 m	Global	ITS (992–1009 bp) N = ?			Lecroq et al. (2009)
41	Shrimp: <i>A. antennatus^d</i>	350–1,500 m	W Mediterranean	16S (547 bp) N = 24–206	X	X	Sardà et al. (2010)
42	Brittle star: <i>Ophionotus victoriae</i>	122–648 m	Antarctic Peninsula to Atlantic sub-Antarctic	16S (~500 bp), COI (560 bp) N = 5–15	X	X	Hunter and Halanych (2010)
43	Molluscs: <i>Alcithoe aillaudorum</i> <i>Chicoreus subpalmatus</i> <i>Chicoreus boucheti</i> <i>Cancellopollia gracilis</i> <i>Cancellopollia</i> sp. <i>Nassaria</i> sp. <i>Sassia remensa</i>	440–665 m 250–300 m 197–438 m 300–790 m 300–790 m 180–730 m 233–487 m	NZ seamounts & continental slope	COI (~650 bp) N = 24 N = 1–22 N = 1–5 N = 1–22 N = 10 N = 4–56 N = 3–19	X X X X X X	 X X	Castelin et al. (2010)
44	Corals, “garden” forming: <i>Stichopathes variabilis</i> Reef building: <i>Enallopsammia rostrata</i> And solitary: <i>Desmophyllum dianthus</i> <i>Stephanocyathus spiniger</i>	122–942 m 489–1,377 m 265–1,150 m 364–467 m	Seamounts & slopes in the Australian & New Zealand region	ITS (300–700 bp) N = 1–9 N = 4–13 N = 5–10 N = 18			Miller, Williams, Rowden, Knowles, and Dunshea (2010)
45	Brittle star: <i>Asteroschema clavigerum^c</i> <i>Ophiocreas oedipus</i> <i>Ophioplinthaca abyssalis</i> <i>Ophioplinthaca chelys</i>	 1,300–2,250 m 1,350–2,300 m 1,650–2,200 m 1,300–2,150 m	NW Atlantic seamounts	16S (421–466 bp), COI (924–1,161 bp) 16S: N = 1–39, COI: N = 1–14, 16S + COI: N = 1–13 16S: N = 1–5, COI: N = 1–5, 16S + COI: N = 1–5 16S: N = 1–27 16S: N = 1–15	 X X X X	 X X X X	Cho and Shank (2010)

(Continues)

TABLE 1 (Continued)

	Study organism(s)	Depth of populations	Geographical location	Details	a	b	References
46	Shrimp: <i>Chorismus antarcticus</i> <i>Nematocarcinus lanceopes</i>	166–410 m 568–2,124 m	Antarctica	COI (~650 bp) N = 3–44 N = 1–91	X	X	Raupach et al. (2010)
47	Protobranch bivalve: <i>Ledella ultima</i>	2,699–4,957 m	Pan-Atlantic (NE, NW, central E and W, SE, SW)	16S rRNA mt (198 bp); N = 4–82	X	X	Etter et al. (2011)
48	Coral, reef building: <i>Lophelia pertusa</i>	140–1,679 m	N Atlantic, Gulf of Mexico to E Atlantic (9,000 km)	9 microsats N = 6–89			Morrison et al. (2011)
49	Coral, solitary: <i>D. dianthus</i>	20–2,395 m	SE Australia, New Zealand, Chile	16S (308 bp), MtC (258 bp) (ITS2) (193 bp) ITS2: N = 9–34, 16S: N = 15–61, MtC: N = 18–52	X	X	Miller et al. (2011)
50	Amphipod: <i>Eusirus perdentatus</i> 1 <i>Eusirus perdentatus</i> 2 <i>Eusirus perdentatus</i> 3 <i>Eusirus giganteus</i> 1 <i>Eusirus giganteus</i> 2 <i>Eusirus giganteus</i> 3 <i>Eusirus giganteus</i> 4	163–930 m 163–930 m 163–930 m 163–930 m 163–930 m 163–930 m 163–930 m	Antarctica	CytB (376 bp), COI (620 bp), ITS2 (457 bp), N = 5–48	X		Baird et al. (2011)
51	Shrimp: <i>A. antennatus</i> ^d	Unclear ≤800 m	Mediterranean, Indian Ocean	16S (546 bp), COI (514 bp) N = 32–58	X	X	Fernández, Heras, Maltagliati, Turco, and Roldán (2011)
52	Giant red shrimp: <i>Aristaeomorpha foliacea</i> ^d	Unknown	Mediterranean to Indian Ocean	ISSR 5 loci, N = 38–51			Fernández, Maltagliati, et al. (2011)
53	Sea spiders: <i>Nymphon australe</i>	156–1,188 m	Antarctica (Peninsula & Weddell Sea)	16S (462 bp), COI (554 bp) 16S: N = 9–5, COI: N = 14–60			Arango, Soler-Membrives, and Miller (2011)
54	Crinoid: <i>Promachocrinus kerguelensis</i> Phylogroup A Phylogroup B	106–541 m 147–1,157 m	Circum-Antarctica	COI (554 bp) Total N = 314 Total N = 107	X	X	Hemery et al. (2012)
55	Polychaete: <i>Hyalinoecia tubicola</i> ^c <i>longibranchiata</i> Squat lobster: <i>Munida gracilis</i>	478–746 m 421–634 m	New Zealand	16S (680 bp), COI (524 bp) 16S: N = 5–12, COI: N = 6–12 COI: N = 4–10			Bors, Rowden, Maas, Clark, and Shank (2012)
56	Bivalves: <i>Acesta sponhi</i> <i>Acesta mori</i>	500–2,088 m 500–3,314 m	E Pacific US	COI (634 bp) N = 3–7 N = 3–33	X	X	Clague et al. (2012)
57	Octocoral: <i>Paragorgia arborea</i>	140–1,525 m	Global	mtDNA (7 genes concatenated): N = 1–35, nuclear (1 locus): N = 3–14, ~3,000 bp total	X		Herrera et al. (2012)
58	Decapods: <i>Plesionika heterocarpus</i> <i>Parapenaeus longirostris</i> <i>Macropipus tuberculatus</i> <i>Munida intermedia</i> <i>Pagurus alatus</i>	~200–500 m ~200–500 m ~200–500 m ~200–500 m ~500–800 m	Atlantic Spain to Mediterranean	COI (512–573 bp), N = 19–26 N = 13–22 N = 20–25 N = 20–25 N = 4–28	X	X	García-Merchán et al. (2012)

(Continues)

TABLE 1 (Continued)

Study organism(s)	Depth of populations	Geographical location	Details	a	b	References
59 Shrimp: <i>A. antennatus</i> ^d	Not specified but presumed to be deep given links with previous studies	Mediterranean and W Atlantic	MtC (369 bp): N = 8–46, AFLP (143 loci): N = 15–46			Lo Brutto, Maggio, Deiana, Cannas, and Arculeo (2012, follow on from Maggio et al., 2009; Roldán et al., 2009; Sardà et al., 2010; Fernández, Heras, et al., 2011)
60 Shrimp: <i>A. antennatus</i> ^d	<800–1,621 m	W. Mediterranean	8 microsats N = 14–55			Cannas et al. (2012)
61 Gastropod: <i>Bursa latitudo</i> <i>Bursa quirihorai</i> <i>Bursina</i> ^c <i>fijiensis</i>	190–600 m 190–680 m 280–602 m	W Indian, W Pacific	COI (566 bp) N = 5–24 N = 7–17 N = 9–16	X X X	X X X	Castelin et al. (2012)
62 Protobranch bivalve: <i>Nucula ataccellana</i>	1,600–3,800 m	NW Atlantic	COI (651 bp): N = 2–30, MAC (254 bp): N = 2–29, CAL (213 bp): N = 2–30, DAC3 (296 bp): N = 2–30, DAC6 (333 bp): N = 2–27.	X	X	Jennings et al. (2013)
63 Giant red shrimp: <i>Aristaeomorpha foliacea</i> ^d	Unclear. From 123 to 1,145 m	Mediterranean, Indian Ocean, NW Australia	COI (685 bp) N = 21–51	X	X	Fernández, Heras, Maltagliati, and Roldán (2013)
64 Deep-water rose shrimp: <i>Parapenaeus longirostris</i> ^d	Unclear. 100–400 m?	Mediterranean	AFLP (143 loci): N = 22–48, MtC: N = 6–17			Lo Brutto, Maggio, and Arculeo (2013)
65 Brittlestars: <i>Ophiomyxa vivipara</i> clade A <i>Ophiacantha vivipara</i> clade C <i>Ophiura ooplax</i> <i>Ophiactis abyssicola</i> <i>Ophiothrix aristulata</i>	82–2,170 m 462–1,408 m 101–1,050 m 350–1,801 m 116–812 m	Australia and New Zealand	COI (580–658 bp) N = 18–56 N = 18–23 N = 7–31 N = 11–72 N = 4–42	X X X X X	X X X X X	O'Hara et al. (2014)
66 Whelk: <i>Buccinum undatum</i> ^d	10–367 m	N. Atlantic	COI (530 bp) + 16S (463 bp): N = 9–93, 5 microsats: N = 7–90	X	X	Pálsson, Magnúsdóttir, Reynisdóttir, Jónsson, and Örnólfsson (2014)
67 Squat lobster: <i>Munidopsis laevis</i>	1,300–1,900 m	W. Pacific	7 microsats: N = 64–92, COI (454 bp): N = 10–43	X		Thaler et al. (2014)
68 Shrimp: <i>P. borealis</i> ^d	Unknown. Found from 100 to 500 m	North Sea, NE Atlantic	9 microsats N = 80–96			Knutsen et al. (2015)
69 Shrimp: <i>A. antennatus</i> ^d	530–750 m	W and central Mediterranean	COI (500 bp), 16S (447 bp) N = 8–48	X	X	Marra et al. (2015)
70 Shrimp: <i>P. borealis</i> ^d	150–3,000 m	W and NE Atlantic, Arctic	10 microsats N = 77–180			Jorde et al. (2015)
71 Octocoral: <i>Callogorgia delta</i>	340–848 m	Gulf of Mexico, Caribbean	9 microsats N = 4–30			Quattrini et al. (2015)
72 Black coral: <i>Leiopathes glaberrima</i>	248–674 m	Gulf of Mexico, Caribbean	10 microsats N = 3–75			Ruiz-Ramos et al. (2015)
73 Lithistid sponges: <i>Neoaulaxinia zingiberadix</i> <i>Isabella mirabilis</i> <i>Neoschrammeniella fulvodesmus</i>	470–1,032 m 270–348 m 470–1,000 m	New Caledonia, east Pacific	ITS (? bp), COI (563 bp) COI: N = 14–18 COI: N = 9–10 ITS1: N = 9–10			Ekins et al. (2015)

(Continues)

TABLE 1 (Continued)

	Study organism(s)	Depth of populations	Geographical location	Details	^a	^b	References
74	Ophiuroid: <i>Ophiothrix</i> sp. III	100–310 m	W Europe	16S (310 bp) N = 7–23	X	X	Taboada and Pérez-Portela (2016)
75	Octocoral: <i>Swiftia simplex</i> ^e	74.7–1,206.3 m	Central E. Pacific (W coast USA)	1,145 SNPs N = 5–7			Everett et al. (2016)
76	Amphipod: <i>Paralicella</i> sp. 1 <i>Paralicella</i> sp. 2	5,329–6,945 m 2,500–6,173 m	Pacific	13 microsats N = 4–24 N = 2–26			Ritchie et al. (2016b)
77	Shrimp: <i>Nematocarcinus lanceopes</i>	Unclear	Antarctica	7 microsats N = 2–78			Dambach et al. (2016)

Number of polymorphic loci displayed is the number used in analyses, not the number sampled from. For Sanger sequenced genes, mitochondrial genes are considered single locus with nuclear genes considered separate loci.

^aWhen a measure of DNA sequence neutrality has been used.

^bWhen evidence exists for at least one population exhibiting non-neutrality.

^cAccording to WoRMS (2016) taxonomic names have changed from the original article.

^dCommercial species.

^eWhere the paper in question designates this species, that is, information not taken from WoRMS.

Microsat., microsatellite markers; Alloz. elect., allozyme electrophoresis; N, number of specimens in binned analyses, detail reported where possible; ISSR, Inter Simple Sequence Repeats; SNPs, single nucleotide polymorphisms; RAD-seq, restriction-site associated DNA sequencing (Baird et al., 2008; Davey & Blaxter, 2010); ?: Unknown.

3 | RESULTS AND DISCUSSION

3.1 | Number and scope of studies

We present a list of 77 publications studying the population genetics of 115 deep-sea benthic species (Table 1). Following a hiatus in the latter half of the 1980s, there has been a steady increase in the yearly rate of papers published: on average, one paper per year (totalling 5) was published in the first half of the 1990s increasing to over five papers a year (totalling 28) in the first half of the present decade (Figure 1). Similarly, the overall number of species examined within these papers has increased from 5 (1 per study on average) in the first half of the 1990s to 48 (1.7 per study) in the first half of this decade. However, the peak in yearly study number was 4 years ago in 2012 with eight publications. The subsequent drop may reflect interannual variability in the number of publications per year, but it may also be an early indicator of a recent levelling off or declining trend in yearly output. It is too early to infer a pattern from the data at this point, but regardless of what the general trend from the present will be a total of 77 studies to date is a relatively meagre sum compared to the vast expanse of the deep-sea realm, which is home to over 25,000 named species (listed in the World Register of Deep-Sea species; Glover, Higgs, & Horton, 2017); a figure that will increase, with the marine biome predicted to house as many as ~2.2 million species (Mora, Tittensor, Adl, Simpson, & Worm, 2011).

The low overall number of studies hampers the ability of researchers to statistically analyse combined data sets and discern general patterns regarding the population genetics of deep-sea fauna. In the most ambitious study of its kind in deep-sea population genetics thus far, Baco et al. (2016) analysed isolation-by-distance (IBD) slopes—a proxy for dispersal distance—from 51 deep-sea studies to reveal patterns of connectivity by depth, taxon, habitat, and

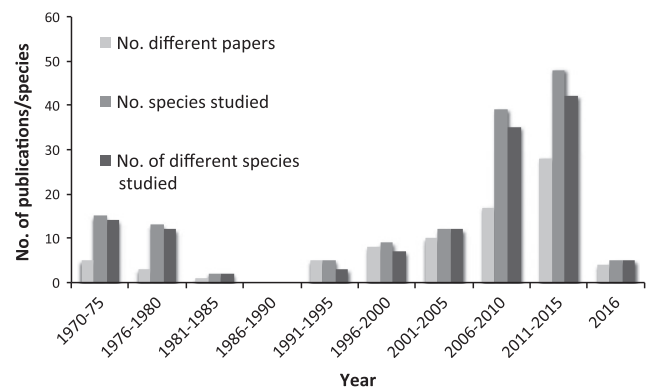


FIGURE 1 Number of publications and number of species over time

life history. A key limitation acknowledged by the authors was the low number of comparable studies, which prevented the use of multivariate statistics, and hence the ability to statistically tease apart confounding variables. Of the 51 studies, only 13 were of non-vent invertebrates. Of those 13 studies, only seven were included here as two we considered demersal, and in four, it was unclear if specimens had been collected from below 200 m. Baco et al. (2016) found that dispersal distances for deep-sea fauna were slightly larger than their shallow counterparts, but they cautioned that taxonomic bias likely skewed the results, as no difference was found within taxonomic groupings. They remarked that many more connectivity studies would be needed to resolve the problem of confounding variables before greater insights from meta-analyses can be achieved.

3.2 | Taxonomic range of studies

The taxonomic breadth of the studies examined herein is heavily skewed towards more conspicuous megafauna, of which,

crustaceans, echinoderms and molluscs account for the majority (Figure 2). Meiofauna (generally considered to be organisms that are above 45 μm in size but under 1 mm) make up a significant component of overall deep-sea diversity (Rex & Etter, 2010), yet are only represented by two studies comprising three species of foraminifera (Lecroq, Gooday, & Pawlowski, 2009; Pawlowski et al., 2007). Of the remaining studies, a substantial proportion (33% of papers published) feature species of commercial interest (Table 2). The earliest such study examined the population genetics of the shrimp *Pandalus borealis* from waters around Iceland and the Denmark Strait using allozyme markers (Jónsdóttir, Imsland, & Nævdal, 1998) and found evidence of population structure across three sites, with recommendations that the three regions (inshore and offshore waters of Iceland and the Denmark Strait) should be treated as separate “biological units” for management purposes. Subsequently, the population genetics of this species has been characterized using allozymes (Drengstig, Fevolden, Galand, & Aschan, 2000; Sévigny, Savard, & Parsons, 2000), random amplified polymorphic DNA (Martinez, Aschan, Skjerdal, & Aljanabi, 2006) and microsatellites (Jorde et al., 2015; Knutsen et al., 2015), spanning the North Atlantic and Arctic continental shelf and slope (see Table 1), providing a wealth of information for stock management. Other commercially exploited species studied include the octopus *Octopus vulgaris* (Maltagliati et al., 2002), the deep-water shrimp *Aristeus antennatus* (Maggio, Lo Brutto, Cannas, Deiana, & Arculeo, 2009; Roldán, Heras, Patellani, & Maltagliati, 2009; Sardà, Roldán, Heras, & Maltagliati, 2010), red crabs of the *Chaceon* genus (Diehl & Biesiot, 1994; Weinberg, Dahlgren, Trowbridge, & Halanych, 2003) and deep-water whelks (Iguchi, Ueno, Maeda, Minami, & Hayashi, 2004; Iguchi et al., 2007). However, just nine studies (12% of total), representing 11 species, have looked at habitat-forming, “ecosystem engineer” species (species that create and maintain habitats; Jones, Lawton, & Shachak, 1994); all were corals (see Figure 3), with the exception of three species of sponge (Ekins, Erpenbeck, Wörheide, & Hooper, 2015). Thirteen studies focused on species that form what the United Nations (UN) terms vulnerable marine ecosystems (VMEs); again these were corals and sponges (see Table 1), which support diverse communities and are

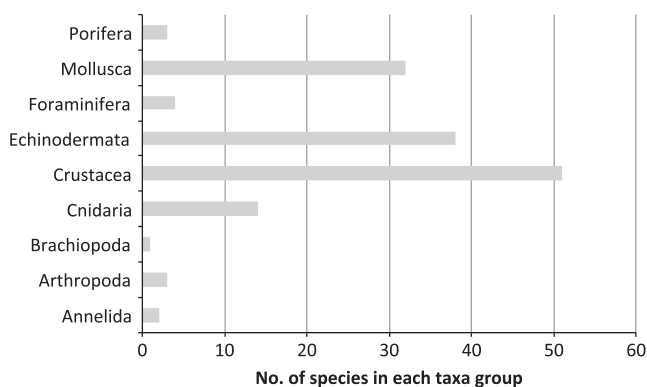


FIGURE 2 Taxonomic scope of deep-sea population genetic studies

considered important for supporting fisheries (e.g., Söffker, Sloman, & Hall-Spencer, 2011). The VME designation for some deep-sea habitats is of particular relevance to national-level resource managers who are obligated by the UN to consider impacts to such sites within their jurisdiction (UNGA 2007, 2009), only adding to the need for more population genetics studies on such species.

3.3 | Depth range and geographical extent of studies

The majority of the studies featured here were shallower than 2,000 m (Figure 4), with a mean maximum study depth of 1,547 m (1,058 m median) and mean minimum study depth of 791 m (380 m median). Most studied species were collected at depths defined as upper bathyal depth (301–800 m; Watling, Guinotte, Clark, & Smith, 2013), which given the relatively shallow depth focus of commercial species harvesting and seafloor mining at present, along with the expectation that sampling costs increase with depth, is unsurprising. However, this depth bias excludes the majority of the planet’s seafloor, which is on average ~3,699 m deep (Charette & Smith, 2010).

Only nine studies sampled species from abyssal depths or greater (abyss defined as 3,501–6,500 m; Watling et al., 2013), with just one study from below 5,000 m (Ritchie, Jamieson, & Piertney, 2016b), an area accounting for approximately a quarter of the planet’s total seafloor. This depth skew has implications for the detection and interpretation of general patterns of population structure in the deep sea, particularly in the vertical plane (to be discussed later). Additionally, with the large-scale mining of abyssal plain polymetallic nodules now imminent, the need for more abyssal population genetics studies is clear. In addition to the depth skew, studies have clustered in certain geographical regions—mostly the Atlantic (Figure 5), with the North Atlantic alone accounting for 18% of all studies. Only five studies can be said to span across entire oceans or beyond. Most studies we consider to be regional (i.e., entirely within ocean subregions defined by climate, currents or basins) or local in scale (studies restricted to small portions of continental slope or within national jurisdictions), with only 17 publications presenting data from more than one ocean region (seven of which were commercial species). The collection of deep-sea specimens is undoubtedly expensive, and the Atlantic focus (48% of studies) reflects the fact that some of the wealthiest developed nations have Atlantic coasts and therefore an Atlantic zone of interest. The Pacific, which is twice as large as the Atlantic, features in only 30% of studies. The Indian

TABLE 2 Breakdown of commercial species population genetic studies

	No. of studies by species	%	No. of papers	%
Commercial species	31	20.95	25	32.47
Non-commercial species	116	78.38	52	67.53

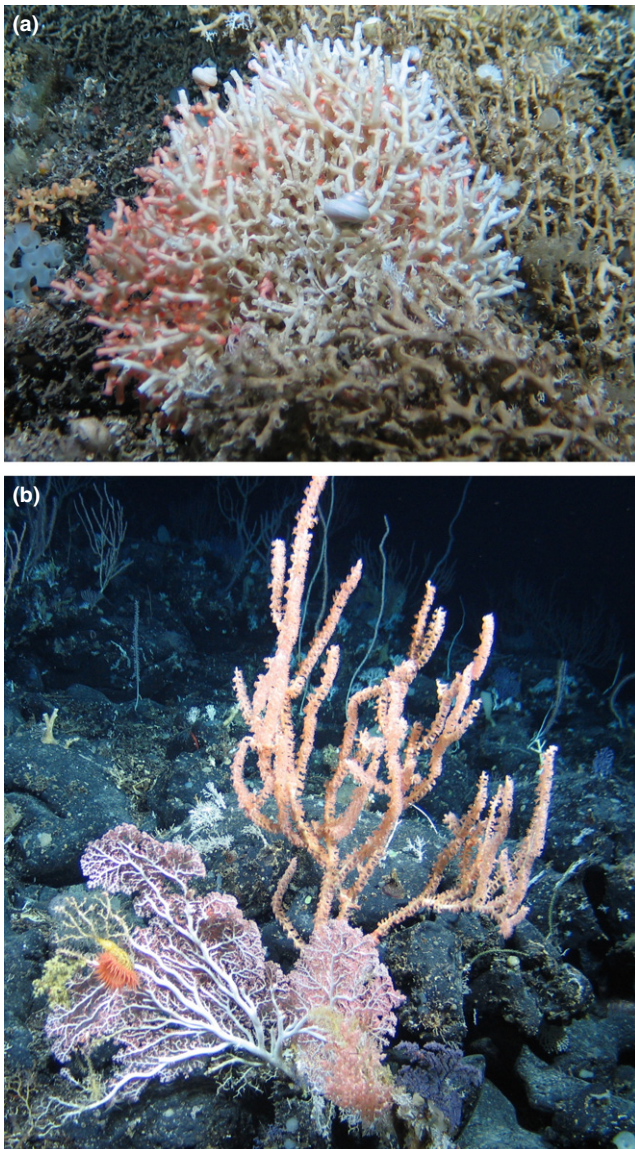


FIGURE 3 Images of deep-sea organisms considered “ecosystem engineers.” (a) *Solenosmilia variabilis*—reef-building coral, (b) a pink *Corallium* fan and an orange bamboo colony. Images taken by Kiel 6000 on JC066 expedition to the SW Indian Ocean

Ocean, which is predominantly surrounded by developing nations, features in just 7% of publications. Unlike the depth skew, this geographical bias almost certainly does not match the geographical intensity of human resource exploitation in these deep-sea regions.

To summarize, studies have been hampered by the difficulties of sampling within the deep sea, limiting the geographical scope, number of sample sites, number of taxa that can be studied (both simultaneously and cumulatively), and number of individuals collected within each sample. Given the financial realities of deep-sea sampling, effort must be focused in the areas that have received the least attention, in terms of depth, regional emphasis and scope, as well as taxa that are considered critically important, either directly as harvested resources, or indirectly as indicators of ecosystem health and functioning.

3.4 | Environmental stability and genetic polymorphism

The earliest study to reference the genetic diversity of any deep-sea taxon was Manwell and Baker (1968) who referred to unpublished allozyme data from the polychaete tubeworm *Siboglinum atlanticum*, showing low genetic variation. Under the widely held assumption of deep-sea environmental stability, this was cited as evidence supporting the hypothesis that populations inhabiting stable environments should exhibit low genetic diversity owing to niche refinement. This idea, later expounded in detail by Bretsky and Lorenz (1970), was itself a theoretical offshoot of the stability-time hypothesis (Hessler & Sanders, 1967; Sanders, 1968), which proposed that environmental stability could explain the apparent high levels of biodiversity encountered in the deep sea as stability allowed greater niche specialization, minimizing competitive exclusion over time and resulting in higher species richness. According to Bretsky and Lorenz (1970), populations in stable environments should exhibit low genetic diversity as a consequence of specialization and refinement; viewed from an adaptive standpoint, changeable environments should “select” for heterozygosity, whereas stable environments should “select” for homozygosity. Although the presumed environmental stability of the deep sea is still open to debate (McClain & Schlacher, 2015), the deep sea seemingly provided a natural testing ground for investigating the influence of disturbance on genetic diversity, prompting the first phase of deep-sea population genetics—spanning the 1970s and early 1980s (see Table 1).

Against initial expectations however, deep-sea populations appeared to exhibit levels of genetic polymorphism similar to shallow-water species, for example, Gooch and Schopf (1972)—a pattern supported by subsequent non-benthic and chemosynthetic studies (see Creasey & Rogers, 1999). Given these results were counter to the prevailing expectation of lower polymorphism in deep-sea populations, a number of explanations were proffered, mostly within a selection paradigm. These focused on allozyme variability as an adaptive strategy to either environmental or trophic stability where “generalist” allozymes were selected against, for example, Ayala, Valentine, Hedgecock, and Barr (1975), or reflected variable adaptive strategies across taxa (Bisol, Costa, & Sibuet, 1984; Costa & Bisol, 1978). Gooch and Schopf (1972) proposed that outside of allozyme neutrality, hybrid vigour (heterosis) could explain high polymorphism across all environments (an idea revisited by Diehl & Biesiot, 1994), but also acknowledged that allozyme polymorphism could be a consequence of sampling subdivided monomorphic populations across depth ranges. Murphy, Rowe, and Haedrich (1976) postulated that high diversity in studied populations reflected a general lack of selective pressure on large, growing populations. This last point, although viewed through a selection prism, emphasized the interplay between demography and diversity. By incorporating a Neutral Theory (Kimura, 1968) framework, Siebenaller (1978) considered demographic size and stability to be important in influencing allozyme diversity in deep-sea populations. From this perspective, special adaptive explanations for deep-sea allozymic diversity were redundant if a significant proportion of allozymes (or other marker allelic

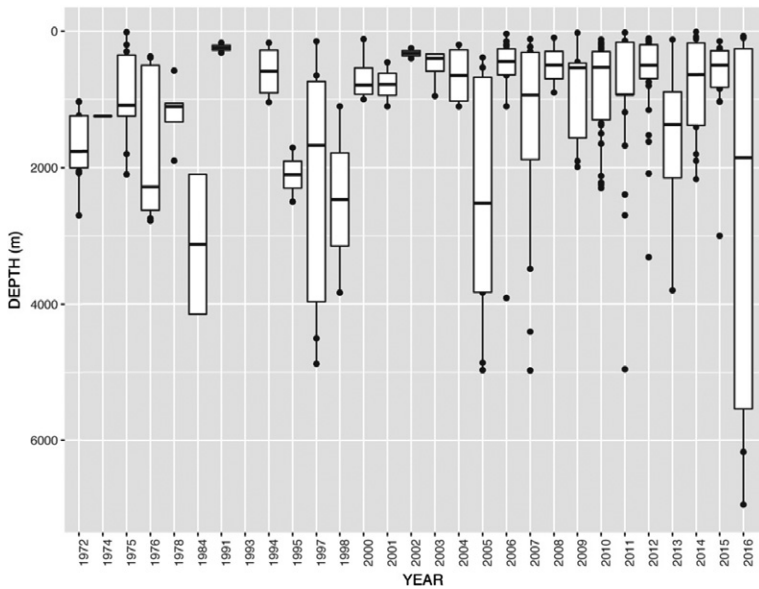


FIGURE 4 Depth range of studies by year. Whiskers extend to 1.5× interquartile range of the data. Black horizontal line in box represents the mean. Dots are outliers

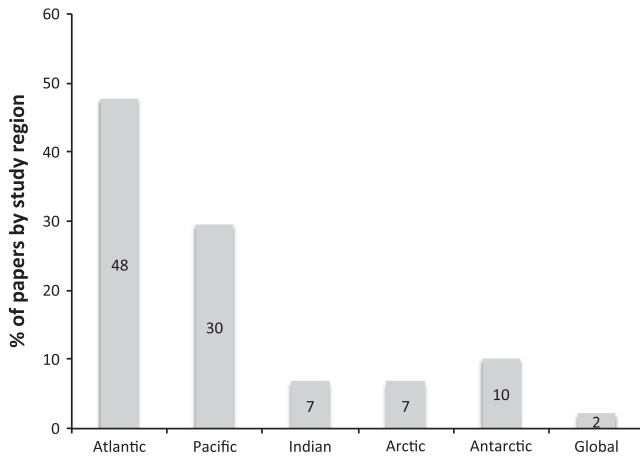


FIGURE 5 Percentage breakdown of publications by geographical region (per cent written in bars)

variants) are selectively neutral, or nearly neutral and if the effects of drift dwarfed that of selection (Kimura, 1968). With the ascendancy of this idea and in the absence of any clear consistent difference between levels of diversity in shallow and deep populations at the time, there was no longer any real impetus for comparing the levels of population genetic diversity between shallow and deep populations. The following decade was notable for the near absence of any deep-sea benthic population genetic studies (Figure 1).

Today, research emphasis has moved beyond the basic question regarding whether or not there are consistent differences in genetic polymorphism between deep-sea and shallow-water populations. Population genetic diversity is now understood to be determined by a range of factors, such as mutation rate, genetic drift, population size, gene flow between population demes, the randomness of mating behaviour, the nature and intensity of selection, as well as the degree of demographic stability over time. In this sense, finding any clear patterns of diversity amidst the noise is a considerable challenge. An early attempt to assess the impact

of environmental stability was undertaken by Costa and Bisol (1978) who compared deep-sea habitats in the NE Atlantic that were presumed to have different levels of disturbance. They found no clear pattern in genetic diversity, although they were not able to quantify the difference in the intensity and periodicity of disturbance at their study sites. Under the premise that hydrothermal vents are more disturbed environments, Creasey and Rogers (1999) compared allozyme heterozygosity between hydrothermal vent and non-vent taxa in the deep sea. They found lower heterozygosity for vent fauna, but it was acknowledged that this pattern could have been confounded by taxonomic differences between vent and non-vent sites. Since then, within vent habitats, higher vent ephemerality (and therefore lower habitat stability) has been linked to lower levels of diversity in some taxa, but the pattern is not universal (reviewed in Vrijenhoek, 2010). Stable refugia have been linked to higher population genetic diversity in non-marine habitats (Brazilian rainforests; Carnaval, Hickerson, Haddad, Rodrigues, & Moritz, 2009), but it remains to be seen if a clear pattern emerges in the marine realm.

Raupach et al. (2010) tested the impact of historical ice scour disturbance on the genetic diversity of two species of Antarctic decapod shrimps; however, with the exception of Costa and Bisol (1978), there have been no attempts to quantify and assess the relationship between genetic diversity and contemporary environmental disturbance in non-chemosynthetically associated deep-sea populations. This is in part due to the difficulties associated with characterizing and quantifying the nature, intensity and periodicity of past and present disturbance events between comparable areas, with similar taxa. However, this is precisely what is required to assess the effects of environmental stability on genetic diversity in the deep sea. Such studies will have direct, practical importance in the assessment of population, species and ecosystem resilience, and would be timely given the encroachment of anthropogenic impacts in the deep sea (mining, Levin, Mengerink, et al., 2016; fisheries, Clark et al., 2015).

3.5 | Patterns of demography

An expectation arising from the notion of deep-sea environmental stability over time would be that populations should be demographically stable and in a state of equilibrium between genetic drift (which removes diversity from a population), mutation and migration (which adds diversity). One way to investigate demographic change within populations is to use neutrality statistics on DNA sequence data to reveal whether there is an excess or deficit of rare genetic variants relative to expectations under conditions of demographic stability and gene neutrality. All but two of the studies (Herrera, Shank, & Sánchez, 2012; Thaler et al., 2014) included here that characterized gene neutrality (26 of 28—92.9%) (Table 1) and 42 of the 56 species

(75%) reveal a departure from neutrality with significantly negative Tajima's D (Tajima, 1989), Fu's F_S (Fu, 1997) or unimodal mismatch distributions for at least one population and gene locus, indicating an excess of rare alleles/haplotypes. This pattern is consistent with demographic bottlenecks followed by expansions (demographic instability), the prevalence of sweepstakes dispersal across patchy habitats (high variance in reproductive success) or selective sweeps (positive selection). The preponderance of non-neutrality in deep-sea populations is noteworthy, as in hydrothermal vent populations it is often attributed to the marked demographic instability expected of metapopulations spanning ephemeral vent fields, where migration–drift disequilibrium is perpetual (as reviewed by Vrijenhoek, 2010). It should be noted, however, that nearly all gene sequence studies

BOX 1 Transitions in genetic tools

The early pioneering efforts characterizing and explaining deep-sea population genetic diversity were limited in the range of analytical tools available, which restricted the scope of questions that could be addressed in this nascent research field. The earliest phase was characterized by the exclusive use of allozyme electrophoresis, with statistics being largely descriptive in nature. Technological advances during the 1980s and 1990s, such as DNA Sanger sequencing (Sanger, Nicklen, & Coulson, 1977), and the development of microsatellite markers, presented researchers with a wider variety of tools to investigate patterns of population diversity and structure. Allozymes continued to be used in deep-sea benthic studies until relatively recently with the first deep-sea benthic paper using Sanger-sequenced genes not being published until 1998 (Chase, Etter, Rex, & Quattro, 1998; Table 1). Gene sequence studies, generally on the mitochondrial Cytochrome Oxidase C subunit I (COI) and/or the ribosomal gene 16S, quickly became popular and remain the most prevalent methodology (Table 3). The advantages of using DNA sequences over allozymes are far from clear cut: allozymes are cheaper than DNA sequencing and also provide statistically more robust multilocus data compared to most DNA sequence studies that are typically single locus. The main appeal of DNA sequence data, however, is the presence of hidden sequence variation not expressed in protein structure, which can provide insights into diversity, patterns of connectivity and demographic history (Parker, Snow, Schug, Booton, & Fuerst, 1998). The analytical and statistical limitations of single-locus data, such as the distorting effects of selection on individual gene loci and their independent genealogies (Brito & Edwards, 2009), have engendered a move back towards multilocus data sets; generally with DNA sequence data or microsatellites (e.g., Jennings, Etter, & Ficarra, 2013; Jorde et al., 2015; Quattrini, Baums, Shank, Morrison, & Cordes, 2015; Ruiz-Ramos, Saunders, Fisher, & Baums, 2015), as the costs of Sanger sequencing and the development and genotyping of microsatellite markers has decreased in recent years.

In addition to the development of a wider range of markers, more bioinformatic tools also became available: innovations in statistical population genetics and the development of “easy-to-use” software packages meant that at the click of a button, population structure could be investigated using measures such as pairwise and AMOVA F_{ST} (summary statistics comparing within and between population diversity; Excoffier & Lischer, 2010). The impact of selective sweeps or recent demographic expansion could also be detected in sequence data using measures of gene neutrality such as Tajima's D (Tajima, 1989) or Fu's F_S (Fu, 1997). In the late 1990s and early 2000s, advances in statistics and computing power allowed researchers to use maximum likelihood or Bayesian inference statistical approaches within a coalescent theoretical framework to model recombination, migration, selection and demographic change over time (Rosenberg & Nordborg, 2002). These innovations have afforded researchers greater insights into the ecology of deep-sea populations and coincided with a greater emphasis on inferring patterns of connectivity in relation to deep-sea topography, hydrography, depth, life history and dispersal strategy (discussed later).

Presently, marine population genetics stands on the cusp of examining population diversity at the genomic level (Luikart, England, Tallmon, Jordan, & Taberlet, 2003; Reitzel, Herrera, Layden, Martindale, & Shank, 2013), using NGS technologies which combine enzyme fragmentation, or selective primer amplification of the genome with high-throughput sequencing to create a large number of single nucleotide polymorphism (SNP) markers. The first population genomic study in the deep sea was published recently (Everett et al., 2016). The particular utility of NGS genomewide data sets for deep-sea researchers is addressed in Box 2.

TABLE 3 Genetic techniques broken down by publication and by species

Genetic markers	Markers by species	Markers by paper
Allozyme electrophoresis	44	23
Gene	88	45
Microsatellite	12	11
AFLP	1	1
RAPD	1	1
ISSR	1	1
Single nucleotide polymorphism	1	1

included here (as well those in hydrothermal vent studies) have used exclusively either one or more mitochondrial genes that are inherently linked and effectively single locus. Only 4 of the 43 gene sequence publications (9.3%) in this review combined the mitochondrial locus with one or more nuclear loci. With only a single locus, it is impossible to differentiate between the effect of selective sweeps and other demographic and life history processes. Indeed, it has been argued that the lack of recombination in the mitochondrial genome leaves it particularly prone to selective sweeps owing to genetic hitchhiking, as compared to genes within the nuclear genome (Bazin, Glémin, & Galtier, 2006). The absence of a clear difference between non-vent and vent populations may therefore reflect a lack of demographic information in single-locus data. The potentially large size of invertebrate populations inhabiting the vast deep-sea floor (or in high density at hydrothermal vents and other biomass hotspots) may also enhance the possibility of selective sweeps, as advantageous mutations are more likely to occur in larger populations (genetic draft). Any demographic or life history inferences gleaned purely from the mitochondrial genome should consequently be treated with caution (Bazin et al., 2006; Galtier, Nabholz, Glémin, & Hurst, 2009; Gillespie, 2000; Gollner et al., 2016). Although a quantitative comparison between vent and non-vent studies has not been performed in this review, the prevalence of non-neutrality (or unimodal mismatch distributions and star-like haplotype networks) in vent studies (Vrijenhoek, 2010), as well as in the studies reviewed here, challenges the assumption that evidence of single-locus non-neutrality in vent populations must therefore reflect the unique conditions of those systems.

Multiple unlinked loci should therefore be better at revealing the signature of demographic change and/or sweepstakes dispersal if all or most loci are broadly in concordance, as selective sweeps occurring independently at the same time could be considered less likely. Studies (both non-vent and vent) using multiple unlinked loci are, however, rare owing to time and cost constraints. In vent populations, a pattern of non-neutrality was found across multiple unlinked loci by Coykendall, Johnson, Karl, Lutz, and Vrijenhoek (2011) and Plouviez, Le Guen, Lecompte, Lallier, and Jollivet (2010) in polychaete worms. Using microsatellites, Roterman, Copley, Linse, Tyler, and Rogers (2016), Teixeira, Serrão, and Arnaud-Haond (2012) and Thaler et al. (2014) were able to show evidence of past demographic

change in vent decapods and molluscs, based on the mismatch between expected heterozygosities estimated from allele frequencies and heterozygosities estimated from the number and spread of alleles. Multilocus studies are equally rare in non-vent research. Jennings et al. (2013) revealed a broad pattern of non-neutrality across five loci (one mitochondrial and four nuclear genes) in an upper continental slope population of the gastropod *Nucula ataccellana*, which was inferred as demographic expansion. In contrast, Miller, Rowden, Williams, and Häussermann (2011) found an inconsistent pattern of non-neutrality between mitochondrial and nuclear loci in populations of the solitary coral *Desmophyllum dianthus*, consistent with demographic stability. Likewise, Herrera et al. (2012) found no evidence of deviations from neutrality for a mitochondrial and nuclear locus in a global study on the deep-water coral *Paragorgia arborea*, but, using a multilocus microsatellite data set, Quattrini et al. (2015) were able to show evidence of a recent demographic bottleneck in the coral *Callogorgia delta*.

With so few multilocus studies thus far, it is difficult to infer broad patterns or draw conclusions regarding the demographic stability of non-chemosynthetically associated deep-sea benthic invertebrates—or to compare them with shallow-water or vent-endemic populations. However, there is preliminary evidence consistent with at least some deep-sea non-vent populations having experienced recent demographic fluctuations; a picture at odds with presumed long-term environmental stability and the presence of populations that are geographically and demographically stable.

3.6 | Migration–drift equilibrium in the deep sea

The consideration of the nature, intensity, and periodicity of environmental disturbance in the deep sea has implications for the assessment and interpretation of population structure as an indicator of connectivity. Population structure only reflects current levels of connectivity within or between populations or subpopulations where genetic drift and migration (and mutation) are in equilibrium. A lack of structure within a population is not necessarily an indicator of panmixia if a range expansion or a post-extinction regional recolonization has occurred following recent disturbance; that is, the similarity between subpopulations is the consequence of sharing ancestral polymorphisms (Slatkin, 1993). Low but significant F_{ST} , indicating weak structure, may not reflect moderate but limited long-term gene flow, but a combination of shared ancestral polymorphisms and recent low-level gene flow, and high F_{ST} could be consistent with a recent resumption of gene flow after isolation rather than long-term minimal connectivity (Marko & Hart, 2012).

The deep sea may be subject to a variety of disturbances that could affect the extent and duration of disequilibrium within and between populations, thus affecting estimates of gene flow. Climate change during and after the Pleistocene epoch has been linked to patterns of demographic/range expansion in a variety of shallow-water marine species, particularly at higher latitudes (Maggs et al., 2008; Marko & Hart, 2012). Deep-sea invertebrates are likely to

have been affected to some degree by changes in regional sea temperature, surface productivity, ocean chemistry and current regime; exemplified in past regional shifts in the dominant foraminifera in deep-sea sediments (Grobe & Mackensen, 1992) and the evidence for post-glacial refugia taxa (Thatje, Hillenbrand, Mackensen, & Larter, 2008). Along with such large-scale climate shifts, populations may be subject to other forms of periodic disturbance, such as seasonal climate and oceanographic fluctuations, or haphazard disturbances, for example, debris flows and turbidity currents (Gage & Tyler, 1991).

Large populations may be particularly prone to disequilibrium as a result of disturbance as the time required for gene flow and drift to equilibrate is proportional to the effective population size (Crow & Aoki, 1984), a condition potentially applicable to marine populations occupying vast habitats with few barriers to dispersal. Marine populations may therefore rarely be at equilibrium over their entire range, as the time required to equilibrate could exceed the general periodicity of perturbation (Grosberg & Cunningham, 2001). The time modelled for the scleractinian *Balanophyllia elegans* to equilibrate after a climate-induced range expansion, for example, was estimated to be >40,000 years; far greater than the time over which climate fluctuations are expected to have affected the species range (Hellberg, 1994). There is no reason to expect that deep-sea populations will be substantially different from shallow-water populations in this respect, and in the absence of data indicating otherwise, one may reasonably expect the prevalence of non-equilibrium conditions. If deep-sea populations are often in a state of disequilibrium, then marine ecologists need to interpret statistics that characterize allele frequencies, such as F_{ST} , with that in mind, or risk inferring gene flow incorrectly (Hellberg, 2009; Marko & Hart, 2012). It has recently been argued that other statistical ways of inferring connectivity that are not reliant on equilibrium conditions should supplement the more traditional methods. Marko and Hart (2012) argue that coalescent-based methods using an isolation-with-migration (IM) framework, which does not assume a state of equilibrium, can complement traditional F_{ST} by modelling an ancestral population splitting in two with subsequent migration (Hey, 2010). The similarities or differences between the results of the two approaches, combined with life history information, can then be assessed to determine the most probable historical and contemporary demographic and geneflow scenario. While the use of such tools has been recently applied in hydrothermal vent studies (Roterman et al., 2016; Thaler et al., 2014), this approach has not yet been applied to any of the studies reviewed herein. Two practical limitations with the IM approach are as follows: first, they are computationally taxing, and second, the constraints of the model may not always be realistic. Furthermore, it has been shown that IM analyses may be prone to false positives if divergence is weak and the number of loci are few (Cruickshank & Hahn, 2014; Hey, Chung, & Sethuraman, 2015). Approximate Bayesian Computing (summarized in Csilléry, Blum, Gaggiotti, & François, 2010) is one of the promising approaches, which avoid the taxing computation of exact likelihood calculations by utilizing summary

statistics and simulations, allowing for more complex, real-world models of migration and demography to be explored.

The extent and duration of disequilibrium within and between populations and demes has consequences for the interpretation of IBD slopes as a proxy of dispersal distance as well. Under conditions of equilibrium with stepping-stone dispersal between nearby demes, pairwise measures of differentiation should positively and linearly correlate with pairwise interdeme distance (Rousset, 1997; Slatkin, 1993) and can be used to infer dispersal distances in the marine environment (Palumbi, 2003). After a recent range expansion, however, the geographical extent of the slope will depend upon the time since the expansion: immediately after an expansion, there will be no slope across the entire geographical range, but over time, depending on the rate of gene flow and the population size, an IBD slope will propagate outwards from any given subpopulation (Slatkin, 1993). With all other things being equal, the ability to detect an IBD slope therefore depends not only on the geographical range of the study, but also the time since any disruption of equilibrium conditions. In their meta-analysis of deep-sea IBD slopes, Baco et al. (2016) acknowledged that the persistence of non-equilibrium conditions would affect individual F_{ST} values, but pointed out that the slope angle, if not the geographical extent of the slope itself should recover quickly under Slatkin's (1993) model. However, when modelling the effects on genetic diversity of non-equilibrium conditions in hydrothermal vent metapopulations, Jollivet et al. (1999) revealed that a persistent, high-frequency state of vent field extinction and recolonization could depress or remove the angle of the IBD slope entirely. Additionally, apparent IBD slopes in other vent taxa on the East Pacific Rise may be the consequence of introgression between divergent populations after secondary contact following regional extinctions along ridge portions, for example, Johnson, Won, Harvey, and Vrijenhoek (2013), Zhang, Johnson, Flores, and Vrijenhoek (2015). Apparent IBD slopes therefore may be illusory or relatively uninformative within metapopulations experiencing frequent disturbance. While hydrothermal vent metapopulations may turn out to be an extreme case, it is conceivable that some non-vent taxa may also exhibit the similar characteristics of metapopulations spanning island-like habitats subject to frequent disturbance, such as those dependent on patchy and ephemeral food bonanzas. The uncertainty regarding the effect of non-equilibrium metapopulation dynamics on the interpretation of IBD slopes, both in vent and non-vent taxa, has the potential to confound nascent attempts to infer broad patterns about dispersal distances from IBD slopes in the deep sea. The problem of how to process and interpret population genetic data generated from populations or metapopulations that are often or perpetually in a state of disequilibrium is beyond the scope of this review, but new modelling approaches that better capture the complexity of the real world—and the software tools that employ them—will be needed to allow population geneticists to objectively and quantitatively assess the most likely of a variety of scenarios of gene flow and isolation.

3.7 | Horizontal and vertical patterns of connectivity/diversity

The earliest study explicitly examining connectivity in the deep sea was by Doyle (1972), who found that brittlestar (*Ophiomusium lymani*) allozyme frequencies on the continental slope off North Carolina varied with depth but not along isobaths. This pattern of population differentiation (or the existence of cryptic species assemblages) along a depth gradient from continental shelf to abyssal depths in benthic fauna has since been observed in an array of other invertebrates including echinoderms (Cho & Shank, 2010), corals (Miller et al., 2011), and molluscs (Etter, Rex, Chase, & Quattro, 2005; Zardus, Etter, Chase, Rex, & Boyle, 2006;). In contrast, inferred horizontal gene flow appears generally extensive at the regional (Clague, Jones, Paduan, Clague, & Vrijenhoek, 2012; O'Hara, England, Gunasekera, & Naughton, 2014), basin-wide (Herrera et al., 2012; Marra, Mona, Sà, D'Onghia, & Maiorano, 2015; Sévigny et al., 2000) and even oceanic scale (Etter et al., 2011; Fernández, Maltagliati, Pannacciulli, & Roldán, 2011). Thus, a general pattern has emerged indicating that vertical divergence between deep-sea populations is far greater than horizontal divergence over similar scales. The mechanisms responsible for this pattern are less clear at present. There may be only minimal (or no) vertical migration of larvae/adults for many species, restricting gene flow and leading to (allopatric) divergence. Alternatively, divergent populations or nascent species may have arisen in allopatry and then made secondary contact occupying niches that happen to be separated by depth. At the other end of the theoretical spectrum, divergence may occur in the presence of high gene flow (i.e., sympatric divergence) owing to disruptive selection (summarized by Bird, Fernandez-Silva, Skillings, & Toonen, 2012). Under this model, differentiation with depth is a result of selective forces operating along steep environmental gradients despite larval connectivity, that is, a form of isolation by adaptation (IBA; Nosil, Funk, & Ortiz-Barrimentos, 2009). In-between allopatric or sympatric divergence is some combination of limited vertical gene flow and selection along environmental gradients resulting in (parapatric) divergence.

A strictly allopatric explanation for the pattern of divergence observed with depth appears at odds with the fact that many invertebrates broadcast larvae capable of vertical travel in the open medium of the marine environment. Etter and Bower (2015) modelled passive larval particle transport with depth along the US eastern seaboard to see whether current patterns in the region were a barrier separating shallower and deep populations in the region, but found this unlikely. Castelin et al. (2012) considered that the existence of sister species of the gastropod genus *Bursa* with overlapping distributions, but slightly different depth bands, the absence of population structure across the ranges, and the lack of any obvious historical barriers to gene flow effectively ruled out allopatric speciation with secondary contact in this case. The prevalence and precise mechanisms involved in sympatric divergence is still a matter of debate amongst evolutionary biologists, but the marine realm may be one of the most likely arenas for the occurrence of selection-driven

divergence in sympatry (Bird et al., 2012). In their study of the widespread Atlantic marine gastropod *N. atacellana* across ~2,000 m depth of the US continental slope, Jennings et al. (2013) found a sharp genetic break in both mitochondrial and nuclear genes at 2,700–2,800 m. Given the lack of horizontal divergence spanning the North Atlantic and the ability of the demersal pelagic larvae to survive for weeks, along with evidence of water mixing at those depths, the authors found it improbable that the reported divergence was the consequence of restricted larval transport. Instead, they considered environmental gradient-driven selection the more likely cause of divergence, which they backed up by noting a similar, parallel pattern for populations in the Southern Atlantic. More recently, Jorde et al. (2015) found that patterns of population structure in the northern shrimp, *P. borealis*, most strongly correlated with bottom water temperature, rather than distance or current strength, consistent with the idea of IBA to environmental conditions.

That being said, however, the presence of divergence or cryptic diversity over short distances or in sympatry can still be consistent with historical allopatric divergence and secondary contact. Divergent genetic diversity within large sympatric morphospecies complexes of sea slugs and amphipods in the Southern Ocean has been attributed to historical allopatric divergence in isolated refugia during historical demographic bottlenecks, possibly related to Pleistocene glacial-interglacial cycles (Baird, Miller, & Stark, 2011; Wilson, Schrod, & Halanych, 2009). Furthermore, not all studies that incorporate depth into their study design have found a pattern of divergence with depth. For example, both Marra et al. (2015) and Sardà et al. (2010) revealed no pattern of differentiation with depth for the Mediterranean shrimp *Aristeus antennatus*, which they ascribed to periodic vertical cascades of cold water down the continental slope facilitating connectivity and the replenishment of harvested shallow populations from deeper refugia, respectively. Both studies were largely confined to upper bathyal depths, which may have constrained the analyses. In a study of global scope, Herrera, Baco, and Sánchez (2010) found no pattern of differentiation with depth with the coral *P. arborea*, which the authors suggested indicative of environmental flexibility, or that the gene sequence markers utilized were incapable of revealing fine-scale genetic structuring with depth.

The depth differentiation hypothesis (DDH; Rex & Etter, 2010) has been proposed to explain the general pattern of population divergence with depth, suggesting that deep-sea population divergence (both vertical and horizontal) should be greatest in the upper bathyal continental slope (200–1,000 m) and reduce with increasing depth towards the abyssal plains. The authors propose that upper bathyal depths have both steeper environmental gradients (e.g., temperature, current speeds, food and light availability) and greater habitat and topographical heterogeneity—both spatially and over time—compared to the more environmentally homogeneous lower slopes and abyssal plains, where few physical barriers to gene flow should exist. A consequence of this elevated divergence, and hence, greater genetic diversity, is that the upper bathyal slopes should be, over evolutionary time, the principle engine generating species diversity in the deep sea, chiming with evidence indicating that the upper

bathyal slope houses the highest species diversity, which declines with towards abyssal depths (Etter & Grassle, 1992; Rex, 1981).

Recent studies specifically examining depth effects on connectivity have tended to support the notion that divergence decreases with depth down the slope, as in the case of gastropods along the west Atlantic slope (Etter et al., 2005), decapod crabs in the Straits of Gibraltar (García-Merchán et al., 2012), and octocorals in the Gulf of Mexico (Quattrini et al., 2015). Other studies, while not explicitly examining changes in divergence with depth, have found genetic discontinuities in the upper bathyal region (e.g., Cho & Shank, 2010; Miller et al., 2011). Some phylogeographical and barcoding studies are broadly consistent with the DDH showing cryptic species breaks at upper bathyal depths, as in the case of the sediment-dwelling isopods in the *Chelator insignis* species-complex off Iceland (Brix, Svavarsson, & Lesse, 2014) and the *Paramuricea* species-complex in the Gulf of Mexico (Doughty, Quattrini, & Cordes, 2014). However, both these studies also found discontinuities at deeper depths as well and others generally found phylogeographical breaks well below upper bathyal depths (e.g., Glazier & Etter, 2014; Havermans et al., 2013; Howell, Rogers, Tyler, & Billett, 2004; O'Hara et al., 2014). Additionally, as patterns of divergence reflect time-integrated processes, absences of genetic discontinuities in individual taxa within specific localities at upper bathyal depths do not in themselves challenge the DDH, which, before its validity can be appraised, will require the accumulation of a great deal more data—across taxa and regions and depth ranges. Therefore, while the evidence for a general pattern of depth-related divergence does seem strong at present, evidence for the DDH must for the time being be considered tentative.

The absence of a universal, clear-cut picture with respect to the effect that depth has on connectivity, divergence, and in the longer term, speciation, highlights the challenges that population geneticists face in attempting to discern patterns in nature—and in particular—within the deep sea. The presence of population structure at any point in time will depend on factors such as species life history, as well as changes to range and demography as a consequence of environmental variability over time and space. Even if structure does exist at a particular moment in time for a particular taxon in a particular location, the ability to detect it will be dependent on both the sensitivity of the markers employed in relation to the taxon in question (which is often unknown) and the geographical scope of the study (both horizontally and vertically), which is often dependent on financial and practical considerations.

The meta-analysis by Baco et al. (2016) represents a first real attempt to integrate and analyse population genetic data from several studies to examine patterns of connectivity within the deep sea. Similar efforts in the future will be essential in determining the validity of the DDH and whether other large-scale patterns can be discerned. However, before this can become possible, more primary studies will be needed to explore divergence with depth at a variety of scales. In the future, accurate, whole and reduced representation genome studies (see Box 2) will afford ever greater insights into divergence across environmental gradients in the deep sea by allowing the detection of fine-scale structure with neutral loci as well as

those under selection (F_{ST} outliers). The promise of accurate reference genomes revealing the location and function of genomic regions under selection will ameliorate our understanding of the process of divergence and speciation in these environments.

The DDH is the counterpart to another pair of related hypotheses regarding the processes influencing patterns of diversity within the deep sea: the source–sink hypothesis (SSH) of abyssal biodiversity (Rex et al., 2005) and its variant the oligotrophic sink hypothesis (OSH; Hardy, Smith, & Thurnherr, 2015)—both of which build on general theories of source–sink dynamics (Holt, 1985). The SSH proposed—based on the depth ranges of mollusc taxa either side of the Atlantic—that many, if not most, abyssal populations are actually dispersal sinks replenished from bathyal depths (Rex et al., 2005). Low population densities in abyssal plains, owing to limited food availability, result in a tendency to Allee effects and therefore local extinctions; abyssal populations are then sustained, replenished or recolonized by immigration from bathyal depths, where greater food availability ensures the viability of populations. While acknowledging that abyssal endemism may be common in some taxa, Rex et al. (2005) suggested that many apparently abyssal taxa may actually be sink populations at the range extremes of largely bathyal taxa. If this is so, then the source of deep-sea diversity in space and time would generally be from bathyal slope depths, a proposal similar to the DDH. To account for regions of high abyssal biomass far from continental slopes, the SSH was modified by Hardy et al. (2015) to include abyssal regions underlying highly productive surface waters as additional sources of larvae to nearby food-limited sinks. Thus, rather than necessarily a slope source to abyssal plain sink, one could think of the eutrophic source to oligotrophic sink instead (OSH). In a global study of ophiuroid diversity, Woolley et al. (2016) revealed species richness in the depth band of 2,000–6,500 m to be generally highest in proximity to continental slopes, consistent with these hypotheses. Evidence for both the SSH (or OSH) is preliminary, with testing these hypotheses a challenge. The SSH does make predictions about patterns of population genetics in the deep sea that have yet to be explicitly tested and can provide new avenues to explore: Rex et al. (2005) proposed that abyssal population haplotype diversity should be lower than at bathyal depths and should generally be subsets of the more common bathyal haplotypes, while analyses of geneflow directionality using coalescent-based methods should generally indicate asymmetric gene flow from shallower to deeper depths. At present, very few studies extend into abyssal depths, with only one from below 5,000 m (Ritchie et al., 2016b), and no study has explicitly modelled gene flow directionality from bathyal to abyssal depths, or from eutrophic to oligotrophic abyssal regions. One aspect of population genetics implied by the SSH hypothesis, but not mentioned by Rex et al. (2005), is that if range expansions often sweep down the slope to abyssal depths, or from eutrophic to oligotrophic regions, then one might expect to see evidence of non-equilibrium dynamics in populations in the form of significantly negative neutrality statistics in sequence markers; something that appears to be common in the studies included here.

BOX 2 The deep-sea dawn of next generation sequencing (NGS)

The great cost and difficulty of sampling in the deep sea has resulted in low sampling effort, hampering the production of high-resolution data sets to assist in conservation and resource management endeavours. Easily (relatively) netted fish, squid and micronekton, such as chaetognaths and krill, alongside species of commercial interest (see Table 1) have been studied in the context of population connectivity. Unfortunately, given the difficulties and limitations of collecting in the deep sea (Ramírez-Llodra & Billett, 2006), it has historically been very difficult (or simply impossible) to gather even modest numbers of individuals (~30) from any given location or region. The minimum number of individuals required for statistically robust analyses is determined by factors such as number of loci and alleles, allele frequency and degree of differentiation (Landguth et al., 2012). However, the low *N* values seen in many historical population genetic studies are far from ideal and often lack statistical power. Future scientific deep-sea expeditions, be they funded in the field of geology, biochemistry, oceanography or biology, should seek to maximize the science possible from their collections through broad interdisciplinary collaborations wherever possible; a key point we hope will be actively supported and advocated by national and international funding agencies. With sound genetic preservation methodologies now being widely available, and relatively simple (see Global Invertebrate Genomics Alliance—GIGA: <http://giga.nova.edu>), alongside advances in next generation sequencing, such networks could propel the field of deep-sea ecology forward at a pace not before seen.

The uptake of DNA Sanger sequencing was relatively slow in deep-sea research. A variety of reasons may explain this, such as a limited availability of DNA sequence primers, as most deep-sea species are non-model organisms (e.g., for Echinodermata; Hoareau & Boissin, 2010), or limited genetic variability, for example, in Anthozoa (Shearer, van Oppen, Romano, & Worheide, 2002), or that budgets have been geared towards the expensive business of specimen collection rather than downstream analyses. One reason for the limited scope of some analyses is that few samples have been historically preserved in a suitable manner for genetic analyses. A large proportion of deep-sea specimens were initially preserved in formalin, before long-term fixation in ethanol. Formalin breaks DNA into small (<200 base pair) fragments, from which only short sequence reads can be generated—if at all (e.g., Etter et al., 2005; Zardus et al., 2006). This limitation has hamstrung the progression of deep-sea population genetics because high-quality DNA is a prerequisite for most NGS techniques that generate high fidelity multilocus genetic data sets. Many of these techniques require high molecular weight DNA with minimal degradation, often from flash frozen or RNALater-preserved samples, for example, Hugall, Hara, Hunjan, Nilsen, and Moussalli (2015). Some studies have been able to adapt NGS methods to utilize the short DNA fragments from formalin-fixed specimens, for example, Tin, Economo, and Mikheyev (2014), but this is far from ideal, relying on reference genomes—something currently not available for deep-sea animals. With the correct preservation techniques, and high-quality genomic extractions, millions of kilobytes of genetic data can now be generated, even in non-model organisms (Helyar et al., 2011), to tackle ecological, evolutionary, physiological, and taxonomic questions, for example, Andrews, Good, Miller, Luikart, and Hohenlohe (2016). To maximize possible scientific output from the future collection of deep-sea specimens, we encourage expeditions to preserve genetic samples according to latest best-practice guidelines with NGS in mind, such as those listed in GIGA.

The ever-reducing cost, heightened efficiency and accuracy of NGS technology means that investigating genetic variation through high-throughput sequencing of genomic DNA is increasingly feasible. Hybridization-based sequence capture and targeted amplification requires a reliable genome assembly (reviewed in Good, 2011) from a suitable taxon: for example, Hugall et al. (2015) used a sea urchin assembly for their ophiuroid studies. However, once an assembly is available, the sequencing of individuals is relatively cheap and the resultant phylogenies and investigations using known genes prove insightful. The potential for such technology, for example, exon recapture methodologies, has already been proven in ophiuroids where well-resolved phylogenies using hundreds of thousands of base pairs per individual are now furthering our understanding of their evolution and biogeography (Hugall et al., 2015).

Whole-genome *de novo* sequencing, however, remains relatively expensive, whereas sequencing sections of DNA randomly spread across a genome is cheaper and does not require previous sequence information. This approach is especially useful for non-model organisms (Gayral et al., 2013); something essential in most marine contexts. There are several NGS methods relevant to population genomics (summarized in De Wit et al., 2012) and depending on whether samples are transcriptome or genome preserved different NGS techniques are possible; RNA-seq (Wang, Gerstein, & Snyder, 2009) for the former, RAD-seq (RAD-seq strategies listed in Toonen et al., 2013) for the latter.

A transcriptome is all the RNA molecules, or transcripts, in a cell (messenger RNA, non-coding RNAs and small RNAs). RNA-seq is a method of using high-throughput sequencing to obtain millions of short reads of RNA (Wang et al., 2009). Should RNA-preserved material be available this technique can reveal patterns of gene expression, provide insights into how genes are regulated, as well being used for population genomics (with the proviso that there will be variable expression rates, sequence contamination etc.). A stumbling block for deep-sea researchers wishing to gain insights into how the deep-sea environment affects gene expression is that

BOX 2 (Continued)

presently, tissue can only be preserved after specimens have been removed from the deep sea and liable to be experiencing physiological stress. A challenge for the future will be to find ways to fix deep-sea organism RNA in situ.

Similar to RNA-seq, and more relevant for the deep sea given that researchers can more easily preserve whole genomes, restriction-site associated DNA sequencing (RAD-seq; Baird et al., 2008; Davey & Blaxter, 2010) combines enzyme fragmentation of the whole genome with high-throughput sequencing to create a large number of genome-wide reads. By adding tags (barcodes) to each sample library (as in RNA-seq) every sequence produced can be traced back to an individual specimen; this also means multiple samples can be sequenced in one run, reducing costs. Both RNA-seq and RAD-seq can be analysed to isolate single nucleotide polymorphism markers (SNPs; Baird et al., 2008). With the dramatic increase in abundance of markers that population genomics offers (100s to 1,000s of SNPs rather than 12–20 microsatellite markers) just 10–20 specimens per population might be sufficient to capture useful information about populations (Willing, Dreyer, & van Oosterhout, 2012), although more is advised. These techniques therefore will be of particular use in deep-sea population connectivity studies (Davey & Blaxter, 2010; Reitzel et al., 2013) where there are usually insufficient sample numbers for statistically robust analyses using traditional markers, such as microsatellites or DNA sequence data sets. The higher resolution of NGS *genome-wide* data sets allows fine-scale patterns of population structure to be examined, something particularly useful when studying inhabitants of an “open” medium such as the ocean. Additionally, whereas microsatellite data must be subjectively genotyped for each study, NGS data, like traditional DNA sequence data, are “future proof” and can be used in conjunction with other NGS data in the future to help build genome assemblies and larger genomic data sets. NGS has also been used to isolate and characterize new microsatellite markers in deep-sea animals where gaining the required high volume and quality of DNA necessary for some NGS approaches, such as RAD-seq, is inherently difficult due to animal size or poor specimen quality (Ritchie, Jamieson, & Piertney, 2016a).

Despite the promise of these technologies, only six marine benthic species have so far had their population connectivity assessed using RAD-seq: the anemone, *Nematostella vectensis* (Reitzel et al., 2013), the American lobster, *Homarus americanus* (Benestan et al., 2015), three species of the coral *Pocillopora* (Combosch & Vollmer, 2015) and the only deep-sea benthic NGS population genomics study, on the octocoral *Swiftia simplex* (Everett et al., 2016). RNA-seq has also rarely been employed in non-model organisms, for example, some pelagic marine fish (reviewed in Hemmer-Hansen, Therkildsen, & Pujolar, 2014); the red abalone bivalve, *Haliotis rufescens* (De Wit & Palumbi, 2013); the green abalone, *Haliotis fulgens* (Gruenthal et al., 2014); and a *Nerita* gastropod (Amin, Prentis, Gilding, & Pavasovic, 2014). In addition, and to highlight the need for species delimitation before population genetic analysis, a comparison of RAD-seq and traditional mitochondrial DNA marker species delimitation has been undertaken on one deep-sea group of Chrysogorgiidae octocoral (Pante et al., 2014).

3.8 | Dispersal strategy and connectivity

Links between dispersal strategy and patterns of population structure in marine environments come with an array of assumptions. Of the species that produce a planktonic larval dispersal phase, those that produce planktotrophic (active-feeding) larvae have historically been considered to have a longer pelagic larval duration (PLD) than those producing lecithotrophic larvae (non-feeding larvae), which in turn confers a greater potential for dispersal and long-range connectivity (e.g., Castelin et al., 2010; Jablonski & Lutz, 1983). However, the evidence for this relationship, although presently accruing, is far from strong (Faurby & Barber, 2012; Mercier, Sewell, & Hamel, 2013; Selkoe & Toonen, 2011; Weersing & Toonen, 2009) with other factors such as larval behaviour, currents, seafloor topography, temperature and uncertainty in PLD and population structure estimates obscuring any signal (Faurby & Barber, 2012; Mercier et al., 2013; Selkoe & Toonen, 2011; Weersing & Toonen, 2009). To add to the complexity, there is evidence that some species have both brooding and non-brooding populations (O'Hara et al., 2014). Recent research also suggests that lower temperatures extend PLDs of

lecithotrophic larvae to a greater extent than planktotrophic larvae (Mercier et al., 2013), potentially muting PLD differences between the two types of larvae in low temperature environments such as the deep sea. To date, very few studies have attempted to estimate PLDs for deep-sea fauna. Just 21 of the 305 species reviewed in Hilário et al. (2015) were exclusively deep sea (from below 200 m depth), and 12 of these were from hydrothermal vents and cold seeps. While having to contend with the same problems of low N and confounding variables as Baco et al. (2016), Hilário et al. (2015) was able to show that deep-sea and eurybathic organism PLD values are significantly longer than those in shallow water.

Despite the recent increase in the number of studies examining connectivity in the deep sea, there is a surprising paucity of deep-sea population genetics studies that have explored the correlation between patterns of population structure and dispersal strategies or other aspects of organismal life history. For example, Castelin et al. (2010) presented a population genetics study of a number of lecithotrophic and direct-brooding gastropod species and one planktotrophic species; the latter had no genetic differentiation over >1,000 km, while others, with potentially weaker dispersal methods,

had structure. In their meta-analysis of IBD slopes, Baco et al. (2016) revealed that feeding larvae dispersed significantly further than non-feeding larvae for their total data set (a pattern that also held when fish were removed), but were unable to show a significant pattern with invertebrates from non-chemosynthetic habitats, most likely owing to the low number of such studies in this subset. Likewise, they also found that pelagic larvae dispersed significantly further than demersal larvae, but not when fish were excluded, and they were unable to tease apart other confounding variables, such as taxonomic bias and life histories. The current predicament, as mentioned before in this review, is that the limited number of deep-sea population genetics studies severely constrains the meta-analysis approach, which will hopefully be a more promising avenue in the future when more deep-sea connectivity and PLD studies become available. Another new method in marine ecology is seascape genetics/genomics (Hansen & Hemmer-Hansen, 2007; Selkoe et al., 2016), which is the integration of oceanographic information, biological parameters of dispersal and genetic analyses to test environmental drivers of genetic structure. While still rare in deep-sea studies, this approach is likely to become more common with the increased use of biophysical models to simulate dispersal patterns in marine fauna (see Ross, Nimmo-Smith, & Howell, 2016). Dambach, Raupach, Leese, Schwarzer, and Engler (2016), for example, were able to reject a simple model of isolation by distance in the Southern Ocean benthic shrimp, *Nematocarcinus lanceops*, instead favouring a model where patterns of connectivity are influenced by the strength of Antarctic Circumpolar Current with asymmetric gene flow. Jorde et al. (2015) showed that Atlantic bottom temperature generally had a greater impact on patterns of population structure in the commercially important northern shrimp, *P. borealis* than larval drift or geographical distance. By combining population genetics with other ecological and physical modelling techniques, studies such as these will not only provide researchers with greater insights into the factors that determine patterns of connectivity between deep-sea populations, but also provide stakeholders with information that could lead to more nuanced ecosystem-based conservation and management approaches in the deep sea.

4 | CONCLUSIONS

Given its compelling status as the largest biome on Earth, we know comparatively little about many deep-sea inhabitants compared to shallow-water or terrestrial fauna. Many paradigms of deep-sea science are still under consideration (McClain & Schlacher, 2015). The purpose of this review has been to collate, characterize and assess the contributions that population genetics studies have made to elucidating the forces and mechanisms that govern life in the deep sea and how this knowledge may be extended and applied in the future.

The most obvious conclusion that can be drawn thus far is the very low number of population genetics studies, given the vast size of the deep-sea realm. A running theme throughout this review has been the way that the lack of primary research has hampered efforts

to infer general patterns regarding the ecology of deep-sea populations. The difficulty in inferring general patterns is compounded by the noticeable taxonomic, geographical and depth bias in the studies examined here, which also leaves stakeholders in large areas of the world with insufficient population genetic information with which to inform their management and conservation strategies. With the ever-increasing encroachment of human activity in the deep sea, it is vital that greater effort is directed towards primary research in deep-sea population genetics.

In spite of the relatively limited number of publications, some broad patterns have still emerged. In contrast with the earliest expectations, there is no clear evidence to suggest that levels of genetic diversity within deep-sea populations are substantially different from shallow-water populations. We found that a majority of the studies that tested for non-neutrality in sequence data revealed patterns of genetic diversity indicative of recent demographic change or selective sweeps, similar to that found in hydrothermal vent fauna, which we found surprising. This could signify that demographic instability is common in the deep sea, or that selective sweeps render single-locus mitochondrial studies demographically uninformative. In the future, we recommend the generation of multilocus data sets where feasible to help distinguish between demography and selection. Nevertheless, there appears to be some evidence challenging the presumption of environmental constancy in the deep sea, and given this, we suggest that researchers operate under the assumption that populations are unlikely to be in drift-migration equilibrium. Assessments of population structure generally reveal extensive horizontal connectivity at the regional and oceanic scale, but limited vertical connectivity, particularly at bathyal depths where there is some evidence consistent with IBA across steep environmental gradients. Some studies chime with the DDH and variants of the SSH, although more investigations will be needed before these hypotheses can be properly appraised.

Moving forward, we consider seascape genetics/genomics to be a promising approach with which to test hypotheses regarding the drivers of population structure in the deep sea. This approach will also be of great utility to stakeholders in managing and protecting marine diversity and resources. Deep-sea population genetics currently stands on the cusp of the next-generation sequencing revolution, which as bioinformatic methods become more sophisticated, will allow researchers to extract more data from a limited number of individuals, a potential boon for a field where the collection of specimens remains the primary challenge.

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DATA ACCESSIBILITY

Data used for analyses are listed in Table 1.

AUTHOR CONTRIBUTIONS

M.L.T. and C.N.R. both designed, executed data analysis and wrote this study.

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