



A review of current knowledge on reproductive and larval processes of deep-sea corals

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Abstract

The presence of corals living in deep waters around the globe has been documented in various publications since the late 1800s, when the first research vessels set sail on multi-year voyages. Ecological research on these species, however, only truly began some 100 years later. We now know that many species of deep-sea coral provide ecosystem services by creating complex habitat for thousands of associated species, and thus are major contributors to global marine biodiversity. Among the many vital ecological processes, reproduction provides a fundamental link between individuals and populations of these sessile organisms that enables the maintenance of current populations and provides means for expansion to new areas. While research on reproduction of deep-sea corals has increased in pace over the last 20 years, the field is still vastly understudied, with less than 4% of all known species having any aspect of reproduction reported. This knowledge gap is significant, because information on reproduction is critical to our understanding of species-specific capacity to recover from disturbances (e.g., fishing impacts, ocean warming, and seafloor mining). It is important, therefore, to examine the current state of knowledge regarding deep-sea coral reproduction to identify recent advances and potential research priorities, which was the aim of the present study. Specifically, this review synthesizes the research carried out to date on reproduction in deep-living species of corals in the orders Alcyonacea, Scleractinia, Antipatharia, Pennatulacea (class Anthozoa), and family Styliasteridae (class Hydrozoa).

Keywords Deep-sea corals · Gametogenesis · Oogenesis · Spermatogenesis · Larval development · Periodicity · Seasonality

Introduction

Over the last few decades, intense research on deep-water corals has expanded our knowledge rapidly, from a basic understanding that there were indeed species living in the

deep ocean to a wealth of data providing ecological, palaeontological, and biogeographical context. Corals in the deep sea gained international attention as their broader ecological role in the world's oceans became more apparent; they are now listed as vulnerable marine ecosystem (VME) indicator taxa (FAO 2009) and several regions currently protect deep-sea corals (e.g., the Northeast Canyons and Seamounts Marine National Monument, USA). Many species are ecosystem engineers (Hennige et al. 2021; Portiño-Ramos et al. 2022) that provide structure, habitat, refuge shelter, spawning, and nursery sites (Husebø et al. 2002; Baillon et al. 2012), and host a wide variety of obligate or transient associates (Krieger and Wing 2002; Buhl-Mortensen and Mortensen 2004; Rowden et al. 2010; Mueller et al. 2013, Baillon et al. 2014a). As such, deep-water corals create hotspots of biodiversity, thus providing important services to both the deep ocean and shallow seas (Roberts et al. 2009; Thurber et al. 2014; Wagner et al. 2020). In addition to the importance of these coral species, their fragility has also been well documented (e.g.,

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Thresher et al. 2015; Taviani 2019; Appah et al. 2022). Without photosynthetic symbiotic algae to provide nutrition (as in zooxanthellate shallow tropical corals), species that live in the deep sea rely largely on marine snow for suspension feeding and consequently grow slowly, typically just millimeters per year (e.g., Druffel et al. 1990, 1995; Risk et al. 2002; Andrews et al. 2005; Roark et al. 2006, Tracey et al. 2007, Sherwood and Edinger 2009; Hitt et al. 2020; Marriott et al. 2020). This makes them highly vulnerable to disturbance, as population recovery and turnover is likely to take from decades to centuries (Prouty et al. 2011, 2016; Baco et al. 2019; Hitt et al. 2020). While there have been several studies highlighting impacts on deep-sea corals, fisheries have by far had the most significant influences on them to date, as these corals frequently co-occur with commercially important fish species (Althaus et al. 2009; Williams et al. 2010; Auster et al. 2011; Clark et al. 2016; Koslow et al. 2001; Watling and Auster 2017; Victorero et al. 2018; Ramirez-Lodra 2020). Additionally, increasing pressures from fossil fuel exploration, oil spills, mineral and mining activities, pollution and shifts in ocean conditions attributable to climate change such as fluxes in temperature, ocean acidification, and deoxygenation are all threats to these sensitive ecosystems (Ramirez-Llodra et al. 2010; Feely et al. 2012; Bostock et al. 2015; Thresher et al. 2015; Clark et al. 2016; Prouty et al. 2016). Research on deep-sea coral health, both present and anticipated (Davies and Guinotte 2011; Anderson et al. 2016; Hitt 2021), is becoming imperative to the management of these species (Anderson et al. 2015; Bostock et al. 2015). Although knowledge has expanded rapidly in recent years, there is still much to learn before corals living in extreme conditions globally can be fully understood.

Reproduction is a fundamental ecological process that every species on the planet must undergo to successfully maintain and expand populations. Detailed knowledge of the productivity of deep-sea corals (age, growth rate, and reproduction) is generally lacking for all but a few key species. While the number of studies on deep-sea coral reproduction has increased rapidly in recent years, there is generally limited data for the various coral groups worldwide with respect to spawning period, fecundity, as well as individual- and population-level variation in reproductive output. There is also an incomplete understanding of larval behavior and settlement, which is particularly important for these species, because they are sessile, meaning that adults cannot migrate from unsuitable and/or changing environments. Consequently, the motile larval stages are the primary means of potential relocation to areas with more favorable conditions to ensure survival of the species. Increased understanding of reproductive parameters can thus help to determine species-specific vulnerability

to various anthropogenic impacts as well as variability in their capacity to recover from these disturbances.

Fortunately, since the earlier reproductive reviews on deep-water scleractinian (Waller 2005) and octocoral species (Watling et al. 2011), there has been a dramatic increase in the number of studies of coral reproductive strategies globally, particularly for the lesser known groups, and thus, it is now imperative to bring these valuable studies together to review. Here, we summarize knowledge of gametogenesis, reproductive seasonality, fertilization, spawning, and larval processes, which in turn will help not only to identify critical knowledge gaps in this field, but also instigate future studies of deep-sea coral reproduction. Furthermore, this review will help to inform and support plans to manage and conserve populations of deep-sea corals worldwide.

Materials and methods

For the purposes of this synthesis, we used several criteria to ensure coverage of relevant taxa of interest to deep-sea coral researchers, and the ability to conduct comparative analysis. A comprehensive review of the literature was carried out to enable a compilation of current information on the reproduction and larval biology of species from the anthozoan subclasses Hexacorallia, Octocorallia, and Hydrozoidina. Orders Alcyonacea and Pennatulacea are used throughout due to their status at time of writing (but see recent suggested changes by McFadden et al. (2022)). We included only azooxanthellate (non-photosymbiotic) species within taxa that are commonly referred to as corals: orders Scleractinia stony corals and Antipatharia black corals from the Hexacorallia; orders Alcyonacea (including both ‘gorgonian’, i.e., skeleton-producing, and ‘soft coral’ species, i.e., lacking a skeleton) and Pennatulacea sea pens from the Octocorallia; and some members of class Hydrozoa, specifically the family Stylasteridae hydrocorals. While the definitions of what constitutes the deep sea can vary widely and it is commonly set to occur below 200 m (average depth of the continental shelf break), we constrained our search to azooxanthellate species that occur in at least 100 m depth to include corals that are either from underrepresented taxa or in genera where comparative analyses could be carried out. Depth range information for each species was obtained from the World Register of Marine Species (WoRMS), the Ocean Biodiversity Information System (OBIS), and the primary literature. All species with known occurrence in waters 100 m or deeper were included, irrespective of collection depth. Biogeographic regions were adapted from Costello et al. (2017) to show regional patterns of study (Fig. 1).

Like many taxa globally, the names of several species reviewed here have changed since their original publications in light of new taxonomic and molecular data. We have used

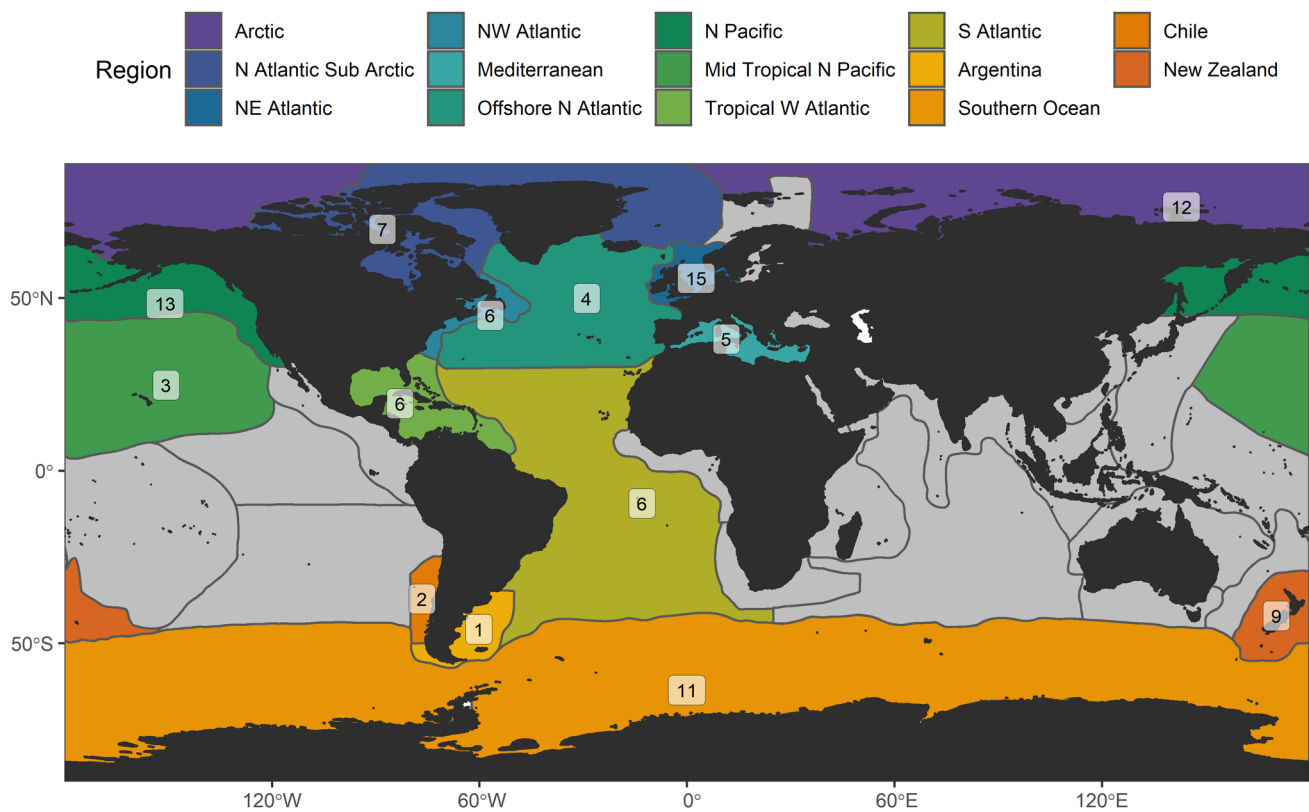


Fig. 1 Map showing the number of deep-sea coral species with reproductive data by region (regions are adapted from marine biogeographic realms reported by Costello et al. (2017)). Colors show regions where the reproduction of deep-sea corals has been studied,

with boxes indicating the number of species per region. Grey shows areas for which no such studies exist. Boxes show number of species per region

the original published species names throughout the text to allow readers to find relevant published material more easily, but have placed an asterisk (*) next to the species names that have been revised more recently than the publication date. Table 1 also contains the revised genus and species names in parentheses.

While larval transport is an important aspect of reproductive strategy in marine species, we have limited this review to the biological aspects of reproduction: gametogenesis, sexual maturity, seasonality, fertilization, and larval development (see Online Resource 1 for definitions). We discuss these aspects of reproduction in four distinct sections: 1) Sexuality and Gametogenesis; 2) Sexual Maturity and Fecundity; 3) Reproductive Mode and Seasonality; and 4) Fertilization, Larval Formation, and Settling. For each section, a general overview is first given, and then, the material is sorted by the five coral taxa groups (Scleractinia, Antipatharia, Alcyonacea, Pennatulacea, and Stylasteridae). Table 1 compiles the reviewed data published up until November 2022 on reproductive and larval traits, a total of 60 publications, and includes only peer-reviewed articles to ensure the integrity of the data.

To determine the total number of described azooxanthellate coral species living in depths below 100 m, occurrence data of each coral group were extracted from OBIS using the package *robis* (Provoost and Bosch 2020) in R (R Core Team 2022).

Discussion

Cnidarians are diploblastic metazoans, lacking a mesoderm and the ability to form organs, and thus, their life cycle is generally simple. Anthozoans and many hydrozoans will generally produce spermatozoa that fertilize an oocyte, which then develops into a planula larva that settles and becomes a primary polyp. Either a colony will develop through asexually produced clonal polyps bound in a matrix or skeleton, or the primary polyp will grow into a larger adult solitary coral. The deep-sea corals examined in the literature all follow this general life cycle, although there are many variations in sexuality (hermaphroditism, gonochorism) and reproductive mode (brooding, broadcast spawning, asexual budding; Fig. 2).

It should be noted, however, that information on any aspect of reproduction is only available for a small fraction

Table 1 Summary of the reproductive processes of deep-sea corals

Taxon	Region	Sexuality	Sex ratio (F:M)	Reproductive mode	Periodicity	Larval nutrition	Larval behaviour	Fecundity	Reference
Scleractinia (Class Anthozoa: Subclass Hexacorallia)									
Caryophylliidae									
<i>Caryophyllia ambrosia</i>	NE Atlantic	H(c)		Broadcast*	AP	L*		200-2750 (PCF)	1
<i>Caryophyllia corniformis (Pramocyathus corniformis)</i>	NE Atlantic	H(c)		Broadcast*		L*			1
<i>Caryophyllia inornata</i>	Mediterranean	G*	1:3.1	Brood		L*			2
<i>Caryophyllia seguenzae</i>	NE Atlantic	H(c)		Broadcast*	AP	L*		52-940 (PCF)	1
<i>Caryophyllia smithii</i>	NE Atlantic	G		Broadcast	P	PL		Several thousand (PCF)	3
<i>Caryophyllia huaiyensis</i>	Chile	G		Brood	AP	L	Swimming		4
<i>Desmophyllum dianthus</i>	Chile	G	1:2	Broadcast*	P	L*		2,488-172,328 (PCF)	5
<i>Goniocorella dumosa</i>	New Zealand	G		Broadcast*	P	L*	Swimming	480 (OPP)	6
<i>Goniocorella dumosa</i>	New Zealand	G		Brood		L*			7
<i>Lophelia pertusa (Desmophyllum pertusum)</i>	NE Atlantic	G		Broadcast*	P	L*		3,300 oocytes/cm ²	8
<i>Lophelia pertusa (Desmophyllum pertusum)</i>	NE Atlantic	G		Broadcast*	P	L*			9
<i>Lophelia pertusa (Desmophyllum pertusum)</i>	Tropical W Atlantic	G		Broadcast*	P	L*			10
<i>Lophelia pertusa (Desmophyllum pertusum)</i>	S Atlantic	G*		Broadcast*	P	L*			11
<i>Lophelia pertusa (Desmophyllum pertusum)</i>	NE Atlantic	G		Broadcast		PL	Swimming		12 & 13
<i>Solenastrea variabilis</i>	New Zealand	G		Broadcast*	P	L*		290 (OPP)	6
<i>Solenastrea variabilis</i>	S Atlantic	G		Broadcast*	P	L			11
Dendrophylliidae									
<i>Balanophyllia elegans</i>	N Pacific	G					Demersal		14
<i>Balanophyllia malouinensis</i>	Argentina	G		Brood				241 (PCF)	15
<i>Enallopsammia rostrata</i>	New Zealand	G		Broadcast*	AP			144 (OPP)	6
<i>Enallopsammia rostrata</i>	S Atlantic	G		Broadcast*	AP				11
Flabellidae									
<i>Flabellum (Ulocyanthus) alabastrum</i>	NE Atlantic	G	1:1	Broadcast*	AP	L*		2800 (PCF)	16
<i>Flabellum (Ulocyanthus) angulare</i>	NE Atlantic	G	1:1	Broadcast*	P	L*		550 (PCF)	16
<i>Flabellum (Ulocyanthus) angulare</i>	NW Atlantic	G	3:1 - 5:1	Broadcast*	P	L*		1,800-10,000 (PCF)	17
<i>Flabellum curvatum</i>	Southern Ocean	G		Brood				1618 (PCF)	18
<i>Flabellum imperatum</i>	Southern Ocean	G		Brood			Demersal	1270 (PCF)	18
<i>Flabellum thoursii</i>	Southern Ocean	G		Brood				2412 (PCF)	18
<i>Monomyces rubrum</i>	New Zealand	G	1:1	Brood			Demersal	17 - ~235 (PCF)	19
Fungiacyathidae									
<i>Fungiacyathus (Bathyactis) marenzelleri</i>	NE Atlantic	G	1:1	Broadcast*	AP	L*		2892 (PCF)	20
<i>Fungiacyathus (Bathyactis) marenzelleri</i>	N Pacific	G	1:1	Broadcast*	AP	L*		1290 (PCF)	21
<i>Fungiacyathus (Bathyactis) marenzelleri</i>	Southern Ocean	G		Broadcast*	AP	L*		2837 (PCF)	22
Oculinidae									
<i>Madrepora oculata</i>	New Zealand	G		Broadcast*	P				6
<i>Madrepora oculata</i>	NE Atlantic	G		Broadcast*	AP			10-68 (OPP); 36-256 oocytes/cm ²	8
<i>Madrepora oculata</i>	S Atlantic	G*		Broadcast*	AP	L*			11
<i>Oculina varicosa</i>	Tropical W Atlantic	G		Broadcast*	P	L*	Swimming		23
<i>Oculina varicosa</i>	Tropical W Atlantic	G		Broadcast			Swimming	1000-4800 oocytes/cm ²	24
Rhizangiidae									
<i>Astrangia danca (poculata)</i>	Tropical W Atlantic	G(h)	1:1	Broadcast	P		Swimming	6000 (PCF)	25

Table 1 (continued)

Taxon	Region	Sexuality	Sex ratio (F:M)	Reproductive mode	Periodicity	Larval nutrition	Larval behaviour	Fecundity	Reference
Antipatharia (Class Anthozoa: Subclass Hexacorallia)									
Antipathidae									
<i>Antipathes griggi</i>	Mid Tropical N Pacific	G*		Broadcast, brood*	L*				26
Myriopathidae									
<i>Antipathella fiordensis</i>	New Zealand	G		Broadcast*	P	L*			27
<i>Antipathella fiordensis</i>	New Zealand	G		Broadcast*	P	L*		1.2-1.73 (OPP)	28
<i>Antipathella wollastoni</i>	Offshore N Atlantic							1-3.09 (OPP)	29
Schizopathidae									
<i>Dendrothopathes grandis</i>	S Atlantic	G		Broadcast*		L*		9 (OPP), 11844 (PCF)	30
Acyonacea (Class Anthozoa: Subclass Octocorallia)									
Acyonidae									
<i>Anthomastus grandiflorus</i>	N Atlantic sub-Arctic	G		Brood		L*			31
<i>Anthomastus (Heteropolypus) ritteri</i>	N Pacific	G		Brood	AP	L	Demersal	5.3 (OPP); 4000 (PCF)	32
Chrysogorgiidae									
<i>Metallogorgia melanotrichos</i>	Offshore N Atlantic	G							33
Corallidae									
<i>Corallium rubrum</i>	Mediterranean	G(h)	1:1	Brood				0.83 (OPP); 435 (PCF)	34
<i>Corallium rubrum</i>	Mediterranean								35
<i>Corallium (Hemicorallium) laevis</i>	Mid Tropical N Pacific	G*		Broadcast*	P				36
<i>Corallium (Pleurocorallium) secundum</i>	Mid Tropical N Pacific	G		Broadcast*	P				36
Keratoisididae									
<i>Acanella arbuscula</i>	NE Atlantic	G		Broadcast*		L*		2.1 (OPP)	37
<i>Keratoisid ornata (grayi)</i>	N Atlantic sub-Arctic	G		Broadcast*	P	L*		39 (OPP); 3 (PRF)	31
Nephtheidae									
<i>Drifa</i> sp.	N Atlantic sub-Arctic	H(f)		Brood			Swimming, demersal		38
<i>Drifa glomerata</i>	N Atlantic sub-Arctic	H(f)		Brood			Demersal	1-1.0 (PPP); 42-2987 (PCF)	39 & 40
<i>Duva florida</i>	NW Atlantic			Brood			Demersal		40
<i>Gersmania fruticosa</i>	N Atlantic sub-Arctic			Brood			Swimming		40
Ellisellidae									
<i>Viminella (Ellisella) flagellum</i>	Offshore N Atlantic	G	3.2:1	Broadcast	AP			7.75 (OPP); 5.62 (PRF)	41
Primooidae									
<i>Antimipatilon antarcticum</i>	Southern Ocean	G	1:1		P			3 (OPP); 17000 (PCF)	42
<i>Dasytenella acanthina</i>	Southern Ocean	G						1.2 (OPP)	43
<i>Famyella rossii</i>	Southern Ocean	G		Brood				1.5 (OPP)	43
<i>Famyella spinosa</i>	Southern Ocean	G		Brood				1.4 (OPP)	43
<i>Primoa notialis</i>	N Pacific	G		Broadcast*				18 (OPP)	44
<i>Primoa pacifica</i>	N Pacific	G		Broadcast*					44
<i>Primoa pacifica</i>	N Pacific	G	1.17:1	Broadcast*		L*		86 (OPP)	45
<i>Primoa pacifica</i>	N Pacific	G	1:1.27	Broadcast				6.1-55.7 (OPP)	46
<i>Primoa resedaiformis</i>	N Atlantic sub-Arctic	G		Broadcast*		L*		84 (OPP, depths < 500 m)	31
<i>Primoa resedaiformis</i>	NW Atlantic	G(h)	1:1	Broadcast*				16.5 (OPP)	47
<i>Thouarella</i> sp.	Southern Ocean	G		Brood				1.1 (OPP)	43
<i>Thouarella variabilis</i>	Southern Ocean	G		Brood		L		1 (PPP)	48
<i>Thouarella variabilis</i>	Southern Ocean	G		Brood	P			1.82 (OPP); 1 (PPP)	49

Table 1 (continued)

Taxon	Region	Sexuality	Sex ratio (F:M)	Reproductive mode	Periodicity	Larval nutrition	Larval behaviour	Fecundity	Reference
Plexauridae									
<i>Dentauricea meteora</i>	Offshore N Atlantic	G	1:92	Broadcast	AP	L	Swimming (stimulated)	5.8 (OPP); 2.93 (PRF)	41 & 50
<i>Paramuricea placomus</i>	NE Atlantic	G							33
<i>Paramuricea placomus</i>	Tropical W Atlantic	G	1:1	Broadcast*				23.4 (OPP)	47
<i>Paramuricea macrospina</i>	Mediterranean	G	1:41	Brood	P			28 (OPP)	51
<i>Swiftia kofoidi</i>	N Pacific	G		Broadcast*				3 (OPP)	44
<i>Swiftia pacifica</i>	N Pacific	G		Broadcast*				4.6 (OPP)	44
<i>Swiftia simplex</i>	N Pacific	G		Broadcast*				42.53 (OPP)	44
<i>Swiftia spauldingi</i>	N Pacific	G		Broadcast*					44
<i>Swiftia torreyi</i>	N Pacific	G		Broadcast*				8 (OPP)	44
Acanthogorgiidae									
<i>Swiftia (Calciogorgia) beringi</i>	N Pacific	G		Broadcast*				13.6 (OPP)	44
Pennatulacea (Anthozoa: Octocorallia)									
<i>Anthophilum grandiflorum</i>	NW Atlantic	G		Broadcast	P	L*		6-31 (PRF); 998-4331 (PCF)	52
<i>Anthophilum murrayi</i>	S Atlantic	G		Broadcast*	AP	L*		90 OPP; 35918 (PCF)	53
<i>Funiculina quadrangularis</i>	NE Atlantic	G	1:1	Broadcast	P			500-2000 oocytes/cm ²	54
<i>Haliperis (Baltica) finnarchica</i>	NW Atlantic	G		Broadcast*	P	L*		6-31 (PRF); 998-4331 (PCF)	55
<i>Kophobelemnon stelliferum</i>	NE Atlantic	G		Broadcast	AP				56
<i>Pennatula aculeata</i>	NW Atlantic	G		Broadcast*	AP				57
<i>Pterocides spinosum (griseum)</i>	Mediterranean	G	1:1	Broadcast*				7-17 (PRF); 27,379-73,114 (PCF)	58
<i>Umbellula encrinus</i>	N Atlantic sub-Arctic	G		Broadcast	P	L*		80-170 (OPP); 1120-6460 (PCF)	59
<i>Umbellula lindahi</i>	Tropical W Atlantic	G		Broadcast		L		2000 (OPP)	60
Stylasteridae (Hydrozoa: Hydrozoa: Anthothecata)									
<i>Cryphelia trophostega</i>	Arctic	G		Brood					61
<i>Cyclotella lamellata</i>	Arctic	G		Brood					61
<i>Distichopora borealis</i>	Arctic	G							61
<i>Distichopora</i> sp.	Arctic	G							61
<i>Errina novaezelandicae</i>	New Zealand	G		Brood*			Demersal		62
<i>Errinopora nameca</i>	Arctic	G		Brood					61
<i>Errinopora pourtalesi</i>	Arctic	G							61
<i>Stylaster brochi</i>	Arctic	G							61
<i>Stylaster campylecus</i>	Arctic	G		Brood					61
<i>Stylaster cancellatus (daskamias)</i>	Arctic	G							61
<i>Stylaster verrillii</i>	Arctic	G							61
<i>Stylaster</i> sp. 1	Arctic	G							61
<i>Stylaster</i> sp. 2	Arctic	G							61

Table 1 (continued)

Species names are given as in the publications cited, with newly accepted species names in parenthesis. Biogeographic regions were adapted from Costello et al. (2017) (see Fig. 1). Symbol and abbreviation meanings are as follows: *Presumed but not confirmed; G gonochoric; G(h) gonochoric, but hermaphroditic instances; H hermaphroditic; H(c), cyclical hermaphroditic; H(f), female-dominated Hermaphroditic; 'Broadcast', broadcast spawning; 'Brood', brooding; P periodic reproduction; AP aperiodic reproduction; L lecitotrophic (non-feeding) larvae; PL planktotrophic (feeding) larvae; OPP Oocytes Per Polyp; PPP Planulae Per Polyp; PRF Potential Relative Fecundity (mature oocytes only); PCF Potential Colony Fecundity. Fecundity estimates for solitary (single polyp) species are shaded. See table footnote for publications denoted by reference numbers

References: (1) Waller et al. (2005); (2) Goffredo et al. (2012); (3) Tranter et al. (1982); (4) Heran et al. (2019); (5) Feehan et al. (2023); (6) Burgess and Babcock (2005); (7) Tracey et al. (2021); (8) Waller and Tyler (2005); (9) Brooke and Järegren (2013); (10) Brooke and Schroeder (2007); (11) Pires et al. (2014); (12) Larsson et al. (2014); (13) Strömberg and Larsson (2017); (14) Altieri (2003); (15) Pendleton et al. (2021); (16) Waller and Tyler (2011); (17) Mercier et al. (2008); (18) Waller et al. (2002); (19) Helzel and Babcock (2002); (20) Waller et al. (2002); (21) Flint et al. (2007); (22) Waller and Feehan (2013); (23) Brooke and Young (2005); (24) Brooke and Young (2003); (25) Szmant-Froelich et al. (1980); (26) Wagner et al. (2012a); (27) Miller (1996); (28) Parker et al. (1997); (29) Rakka et al. (2017); (30) Lauretta and Penchaszadeh (2017); (31) Mercier and Hamel (2011); (32) Cordes et al. (2005); (33) Simpson et al. (2005); (34) Priori et al. (2013); (35) Torrents et al. (2005); (36) Waller and Baco (2007); (37) Beazley and Kenchington (2012); (38) Sun et al. (2010a); (39) Sun et al. (2010b); (40) Sun et al. (2011); (41) Rakka et al. (2021a); (42) Orejas et al. (2002); (43) Orejas et al. (2007); (44) Feehan and Waller (2015); (45) Waller et al. (2014); (46) Waller et al. (2019); (47) Fountain et al. (2019); (48) Brito et al. (1997); (49) Guardiola (2014); (50) Rakka et al. (2021b); (51) Grinyó et al. (2018); (52) Baillon et al. (2014b); (53) Pires et al. (2009); (54) Edwards and Moore (2009); (55) Baillon et al. (2015); (56) Rice et al. (1992); (57) Eckelbarger et al. (1998); (58) Garcia-Cárdenas and López-González (2022); (59) Hamel et al. (2020); (60) Tyler et al. (1995); (61) Brooke and Stone (2007); (62) Miller et al. (2004)

of species known to occur at depths below 100 m (Fig. 3A). While the numbers vary considerably across taxonomic groups, overall, less than 4% of all known deep-sea corals have had some studies on reproduction completed, and thus, patterns can be hard to elucidate. Comparing the 3.5% of deep-sea scleractinian species that have been examined to the roughly 50% species coverage of shallow tropical scleractinians (Harrison 2011), it is clear that we are quite far from having even a broad understanding of deep-sea coral reproductive processes.

Despite the limited available data, there has been an encouraging increase in the number of studies on deep-sea coral species since the 1980s, with the majority of current studies having been published in the last 2 decades (Fig. 3B). The most recent review of reproduction in deep-sea scleractinians (Waller 2005) looked at just 15 species, whereas we include 22 in this synthesis. Similarly, the latest review of deep-sea octocoral reproduction (Watling et al. 2011) examined 20 species, whereas we examine 35 herein.

The growing literature on deep-sea coral reproduction is still plagued by a number of biases. For example, although there is regional coverage in most taxa (Fig. 1), the stylasterids have only been studied from the Arctic and New Zealand regions, with a single study (Brooke and Stone 2007) covering 12 of the 13 species that have been examined. Additionally, there are substantially more studies from the North Atlantic than any other basin (Fig. 1), likely owing to the Exclusive Economic Zones of Europe, Canada, and the United States bordering this region where there are a large number of investigators focused on reproductive research.

Depth-related trends show that, across all coral taxa, most species have an upper depth range of 500 m or shallower, with very few species exhibiting depth ranges that begin below 1500 m (Fig. 4). The disparity between depth ranges and actual study depths should be noted as well, since the majority of studies are carried out at or close to the species' shallowest extent. This is, no doubt, a factor of collection, particularly in the case of deep-water emerged species, such as *Antipathella fjordensis* (Miller 1996), *Primnoa pacifica* (Waller et al. 2014), and *Desmophyllum dianthus* (Feehan et al. 2019). The high cost of research cruises and equipment capable of sampling below 1000 m frequently precludes extensive and/or seasonal sampling. Moreover, the generally decreasing biomass of species with increasing depth makes collecting sufficient sample sizes for reproductive studies at depth difficult. While punctual studies provide valuable information for understanding reproductive function in a species, multi-site studies may be more informative, since population-level differences in reproductive processes have been reported in species from both shallow water (reviewed in Harrison 2011) and deep water (Waller et al. 2002, 2019; Flint et al. 2007; Waller and Feehan 2013; Baillon et al. 2015; Johnstone et al. 2021). Only 11 of the 71 species

Fig. 2 Simplified general model of the life cycles of deep-sea corals. Different development phases have been used to illustrate the diversity ascribed to the taxa discussed in this manuscript

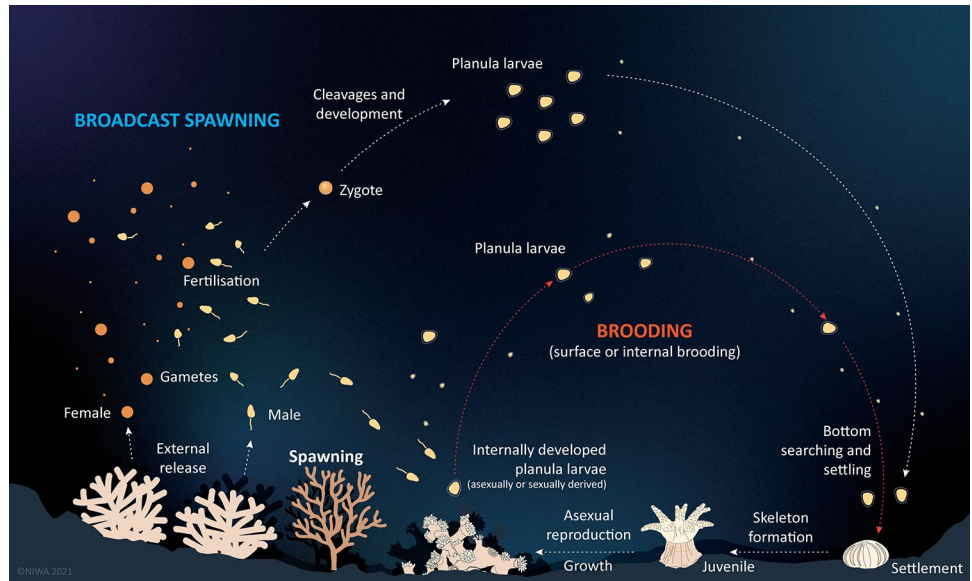


Fig. 3 **A** Total number of coral species with ranges extending below 100 m depth by taxonomic group and the number of species with published reproductive data (grey) and with no available reproductive data (hatched). **B** Cumulative number of studies over time by taxonomic group. Note that values represent published studies, irrespective of species (i.e., different studies of the same species are each shown)

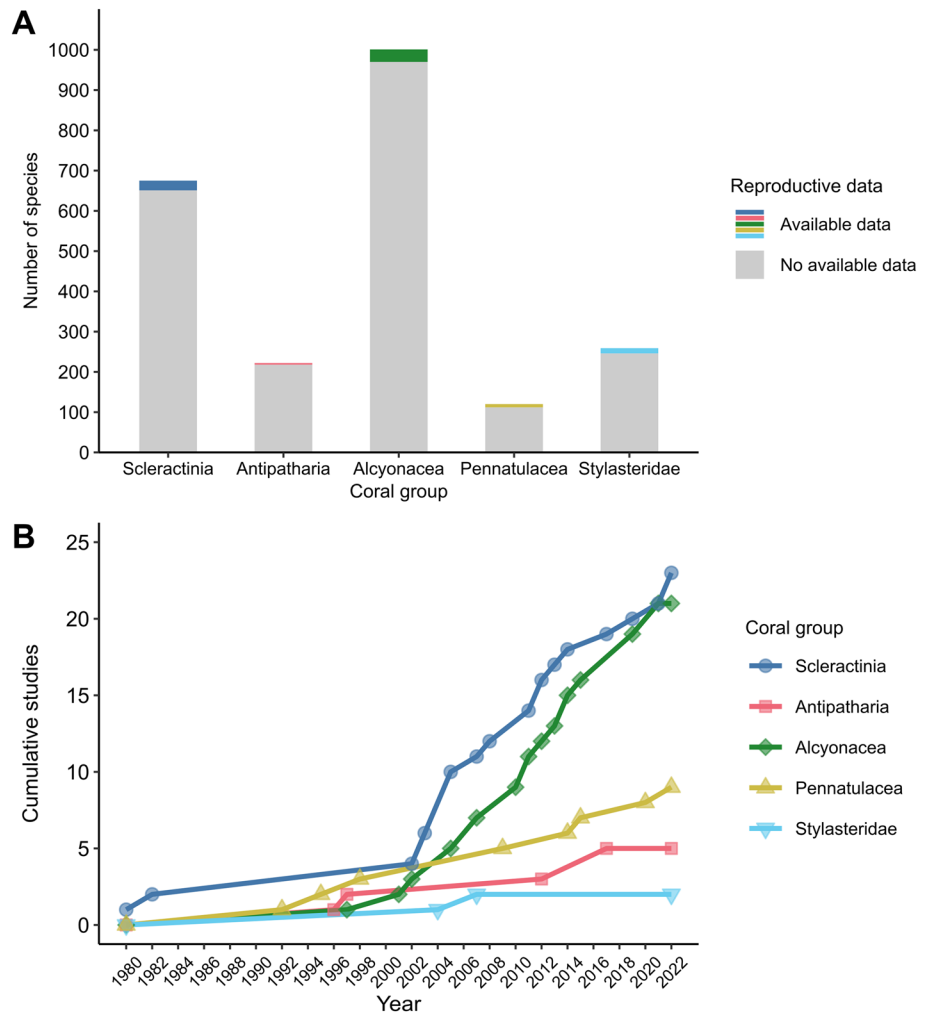
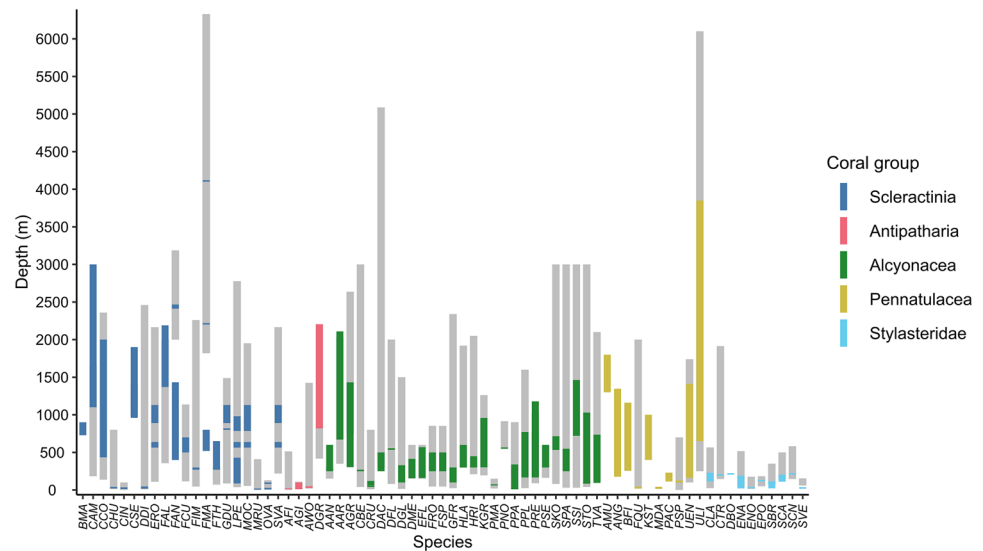


Fig. 4 Known depth ranges of all coral species examined in this review (grey). Colored areas represent the depth ranges where reproductive information has been published across each taxa. Species names have been reverted to three letter codes (first letter is the first letter of the genus; second and third letters are taken from species name). Please see Table 1 for full details of species



included in this review have been sampled from more than one location.

Below, we have examined the various reproductive aspects of deep-sea coral life cycles with a description of general trends followed by features specific to each taxonomic group (Scleractinia, Antipatharia, Alcyonacea, Pennatulacea, and Stylasteridae).

Sexuality and gametogenesis

Cnidarians are basal, radially (or biradially) symmetrical organisms that are organized into distinct tissues but lack true organs and thus have no sexual glands or gonads (despite the widespread use of the term in the literature). As such, it is impossible to tell male from female coral colonies (or polyps) unless sexual reproduction is ongoing through the production of gametes, however even then, particularly in the Scleractinia, sexes are difficult to distinguish, because gametes usually cannot be viewed without dissection or histological analysis. Gonochorism (the occurrence of separate sexes) is by far the most common sexual strategy across all taxa examined, with hermaphroditism (both sexes within a single individual) appearing only within the Scleractinia and the Alcyonacea (Fig. 5). For the scleractinians, this pattern differs from that observed in shallow zooxanthellate species, where hermaphroditism dominates (Harrison 2011), but is similar in shallow octocorals (Kahng et al. 2011). Hermaphrodites that have been identified in deep-sea corals have either been female-dominated or cyclical (where there is constant cycling of sexes within a single coral, with one sex being dominant at one time), alongside rare instances of aberrant hermaphroditism reported in gonochoric species of both Alcyonacea and Scleractinia. Determination of sexuality is dependent, however, on sampling effort (i.e., having

sufficient samples to thoroughly assess patterns across space and time), and this is lacking in a number of the studies compiled in the present review.

Coral polyps are made up of two layers separated by mesoglea, i.e., the ectoderm and the endoderm, and gametes first develop from interstitial cells along the mesenterial filaments during the reproductive period (Farrant 1986). Interstitial cells are formed from ectodermal cells in the Stylasteridae, and endodermal cells in the Scleractinia, Antipatharia, Alcyonacea, and Pennatulacea (El-Bawab 2020). During the reproductive period, these cells form oogonia or spermatogonia that go through several stages before reaching maturity. Unlike other cnidarians (El-Bawab 2020), deep-sea corals have not been studied extensively to elucidate gametogenesis at levels beyond paraffin histology, although some patterns have been discerned from the more well-known coral taxa. In all deep-sea corals studied to date, spermatogenesis occurs within spermatocysts (spermatocysts), which are clusters of spermatocytes that undergo mitosis and meiosis to form spermatids, enclosed within a membrane that either breaks and releases mature spermatozoa into the gastrovascular cavity prior to spawning (e.g., in *Lophelia pertusa**, Larsson et al. 2014), or dissolves and releases mature spermatozoa directly in the water column upon spawning (e.g., *Pennatula aculeata*, Eckelbarger et al. 1998). Through mitosis and meiosis, sperm cells become progressively smaller and more abundant as they develop, undergoing flagellar development and a condensation of chromatin into the eventual pointed head shape of mature spermatozoa (Fig. 6; Johnstone et al. 2021). Histological sectioning has previously been used to determine stages of spermatogenesis based on gross morphology (e.g., Waller et al. 2005; Mercier and Hamel 2011; Baillon et al. 2014b), as well as measurements of spermatocysts (e.g., Cordes et al. 2001; Rakka et al. 2021b); however, recent findings indicate

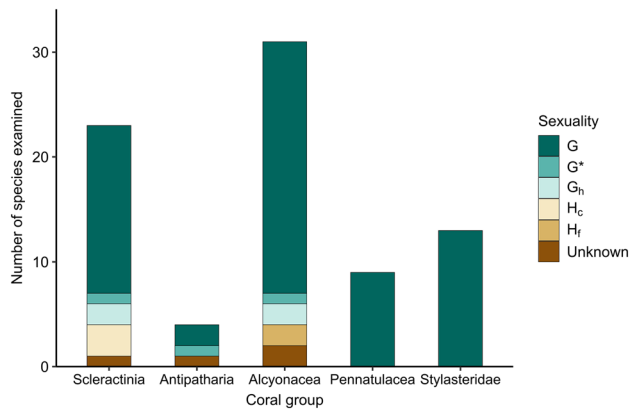


Fig. 5 Breakdown of sexuality types shown in deep-sea coral species examined to date. *G* Gonochoric; *G**, Presumed gonochoric; *G_h*, Gonochoric with occasional hermaphrodites; *H* Hermaphrodite; *H_c*, Cyclical Hermaphrodite; *H_f* Female-dominated hermaphrodites

that measuring head shape and nuclear diameter may be a more accurate way of assessing stages of spermatogenesis (Johnstone et al. 2021). Measuring sizes of spermatocysts may provide inaccurate data on development, because they are not single cells (like oocytes), spermatids undergo mitotic and meiotic processes (splitting and shrinking) during development, and they lack central markers to base a measure of diameter from (like the nucleus in oocytes).

Oogenesis follows a similar general pattern in deep-sea coral taxa. Small oogonia with large nuclei bud from the mesentery and undergo several stages (see Mercier and Hamel 2011), starting as previtellogenic oocytes before accumulating yolk during vitellogenesis (Fig. 6). In later stages, oocytes form a cortical granular layer (presumed, given the absence of transmission electron microscopy studies), which is a layer of organelles associated with the prevention of polyspermy. In all but the final stages, the nucleus (germinal vesicle) is large and relatively central, but in the final stages, it moves to the edge of the oocyte and eventually disperses (Feehan et al. 2019). Measuring oocytes has become the standard method for understanding how oogenesis proceeds and is also indirectly used to elucidate spawning periodicity. Accurate measurements of oocyte diameters on histological sections require finding a central point, i.e., only measuring oocytes with a visible nucleus, and using Feret diameters to account for misshapen oocytes.

Corals may also undergo asexual, or agametic, reproduction, where there is no fertilization and asexually derived propagules or fragments of parent colonies are able to colonize new locations. All colonial species of corals increase colony sizes by producing new polyps through inter- or intra-tentacular budding; however, there have been only a few direct observations of dispersive asexually produced propagules in deep-sea corals.

Scleractinia

These corals occur in two major forms, either as solitary corals (often called cup corals), thought to be genetically distinct individuals or clumps of individuals, or complex colonial branching reef-like species comprised of many clonal polyps. As with the other taxa described in this review, the scleractinians are primarily gonochoric, but three hermaphroditic species of solitary cup corals have been identified. Species of *Caryophyllia* (family Caryophylliidae) undergo cyclical hermaphroditism, where individuals were determined to cycle through maturation of male and female gametes, as either spermatogonia and vitellogenic oocytes were observed on the same mesenteries, or conversely oogonia were present on a mesentery that also contained mature spermatocysts (Waller et al. 2005). Aberrant hermaphrodites have also been found in gonochoric species (Szmant-Froelich et al. 1980; Pires et al. 2014).

Gametogenesis in deep-sea scleractinian species appears to follow the general patterns highlighted above (Fig. 6) and has been well described from several species within three families sampled from different global populations: *Lophelia pertusa**, family Caryophylliidae (Waller et al. 2005; Brooke and Järnegren 2013), *Flabellum angulare**, family Flabellidae (Mercier et al. 2011; Waller and Tyler 2011), and *Fungiacyathus marenzelleri**, family Fungiacyathidae (Waller et al. 2002; Flint et al. 2007; Waller and Feehan 2013). Gametogenesis in these species was found to remain constant among intra-specific populations sampled from different environments; however, intra-specific differences in periodicity and fecundity were found (see ‘Reproductive Mode and Seasonality’).

Asexual reproduction in the form of fission has been observed in the species *Fungiacyathus marenzelleri** (family Fungiacyathidae) in the Northeast Atlantic, although at very low incidence, suggesting sexual reproduction was still dominant in this species (Waller et al. 2002). This remains the only report of directly observed asexual propagation to date in deep-sea solitary scleractinians, but genetic studies have suggested that asexual reproduction may be an important mode of reproduction in reef-building species, albeit potentially influenced by anthropogenic impacts, such as deep-sea trawling in studied reef ecosystems (LeGoff-Vitry et al. 2004; Morrison et al. 2011; Dahl et al. 2012; Miller and Gunasekera 2017). Indeed, fragmentation is common in shallow scleractinians, as is ‘polyp bail out’ (where polyps detach from the parental colony to settle as new individuals), fission, budding, and the parthenogenic production of larvae (see Harrison 2011). It is therefore possible that deep-sea scleractinian taxa similarly undergo various forms of asexual reproduction that have yet to be documented.

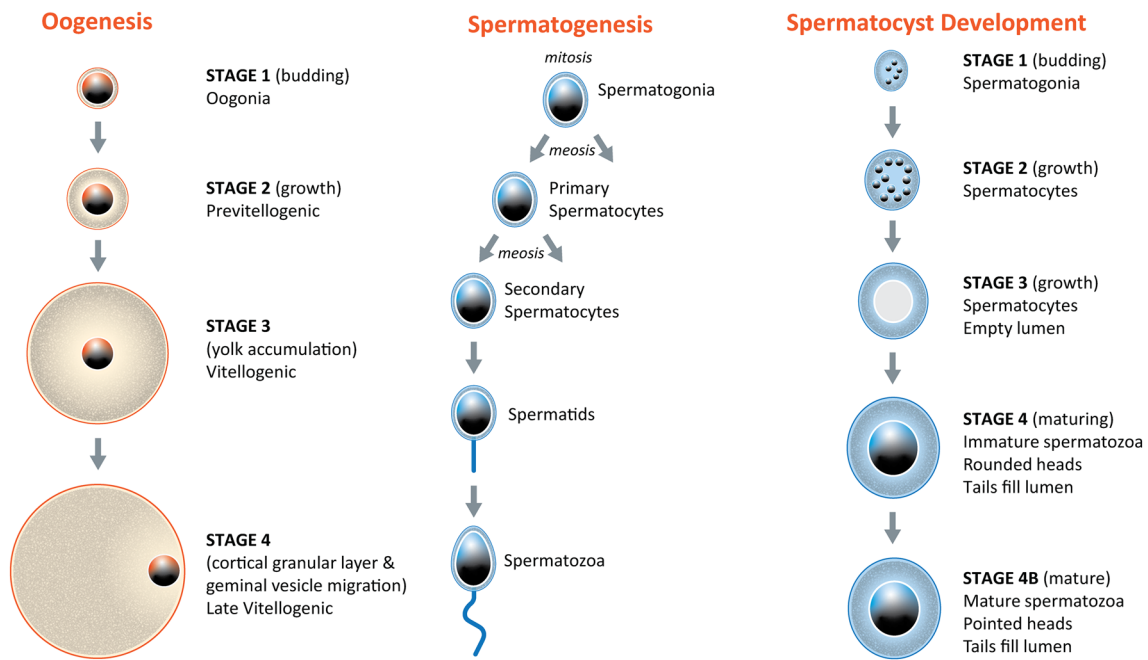


Fig. 6 Simplified illustration of oogenesis, spermatogenesis, and spermatocyst development in deep-sea corals

Antipatharia

Reproductive investigations have been conducted for approximately 20% of the total number of described antipatharian species, although a majority of these are from individuals sampled in shallow water (Wagner et al. 2012b). All species of antipatharian examined to date are gonochoric, whether they are from shallow or deep-water areas (Wagner et al. 2011; El-Bawab 2020). One shallow species was shown to display dimorphic sexuality, with differing polyps being either male or female (Gaino and Scoccia 2010), highlighting the overall importance of investigating multiple polyps from single colonies. It should also be noted that nearly all previous studies of reproductive modes in antipatharians have collected samples over a short term (i.e., < 1 year), and thus, sequential hermaphroditism, where individuals change sex over time, cannot be ruled out as a reproductive strategy (e.g., Wagner et al. 2012b).

Gametogenesis in deep-sea Antipatharia species appears to follow general patterns (Fig. 6). Only two of six primary mesenteries bear filaments (and can thus be reproductive), and these are easily distinguished as the longer lateral tentacles that also characterize this order (Wagner et al. 2012b). As gametogenesis progresses in both males and females, the base of the lateral tentacles visibly enlarges, so it is often possible to distinguish reproductive individuals visually. For example, mature colonies of *A. fordensis* (family Myriopathidae) can be identified by the presence of orange,

swollen polyps as oocytes become ripe just before broadcast spawning (Parker et al. 1997).

Alyconacea

Deep-sea alyconaceans are either gonochoric or hermaphroditic, with three modes of reproduction being described: broadcast spawning, internal brooding, and surface brooding. Hermaphroditism is a rare reproductive mode in the Alyconacea, particularly in deeper living species where it is most frequently seen as an aberrant condition in a single colony (Watling et al. 2011; Priori et al. 2013; Fountain et al. 2019). Some alyconaceans, such as *Anthomastus ritteri**, have dimorphic polyps, where only the siphonozoids are reproductive (Cordes et al. 2001), as opposed to the majority of species that reproduce only through the autozoid polyps. Shallow corals from the family Paragorgiidae are thought to have gametes present in both autozoids and siphonozoids (Bayer 1973). As yet, no deep-water species of Paragorgiidae have been examined for reproduction; however, Lacharité and Metaxas (2013) suggest that *P. arborea* is a brooder based on recruitment and abundance.

Stages of gametogenesis follow the general model described earlier (Fig. 6), with clusters of gametes often attached to mesenteries with pedicels or stalks and presumed accessory cells surrounding the gametes (Kahng et al. 2011; Watling et al. 2011; Beazly and Kenchington 2012; Waller et al. 2014). As the gametes increase in size, they bulge into the gastrovascular cavity, and oocytes tend to be large

and yolky (Watling et al. 2011). Oosorption, where not all oocytes develop to maturity and are instead reabsorbed by the polyp, has been reported as both an environmental stress response (e.g., *Primnoa pacifica*, Rossin et al. 2019) and as a possible way to gain adequate nutrition to support ongoing oogenesis (e.g., *Keratoisis ornate**, Mercier and Hamel 2011). Indeed, as gametes bulge into the gastrovascular cavity when reaching maturity, it has been hypothesized that feeding capability would be diminished, and so, oosorption of excess oocytes may be essential for completing gametogenesis (Watling et al. 2011).

Agametic reproduction is also frequent in alcyonaceans, both in deep and shallow environments, and it is the primary method of colonial growth through intra-tentacular (where the polyp divides itself into two new polyps) or extratentacular (where a new polyp forms between polyps) budding. While sexual reproduction is the primary mode of dispersal and genetic mixing in alcyonaceans, asexual propagation can play an important role in population dynamics. Asexual propagation in corals is usually through fragmentation, where polyp-bearing fragments detach from the mother colony and regrow in a new location. Although this strategy is relatively common in shallow reef-building scleractinians (and has been inferred for deep reef-builders such as *Lophelia pertusa** using population genetic techniques, Dahl et al. 2012), it has also been reported in shallow alcyonaceans (Lasker 1990; Dahan and Benayahu 1997) and thus likely occurs in deeper dwelling species. Small colonies have frequently been observed at the base of large alcyonacean colonies that may well represent the outcome of fragmentation (authors' pers. obs.).

Although polyp-bail out was once thought to be restricted to scleractinians or antipatharians, it has recently been observed in two species from two families of cold-water alcyonaceans, *Acanthogorgia armata* (family Paramuriceidae) and *Acanella arbuscula* (family Keratoidididae), kept in the laboratory (Rakka et al. 2019). This method of asexual reproduction is usually (but not always) associated with extreme environmental stress, leading to 'reverse development', where colonies expel polyps, mimicking the release of a planula, leaving their original colony to die. It is unknown how common this strategy is in deep-sea octocorals, and given the difficulties in culturing deep-sea gorgonians in the laboratory, it is likely to be under-reported.

There are few examinations of deeper living corals from different locations to assess whether patterns of sexuality and gametogenesis might change with environmental conditions, as is (rarely) seen with shallow species and generally attributed to potential cryptic or sibling species (see Kahng et al. 2011). Alcyonaceans with broad depth ranges would, however, be expected to experience significant changes in energy available to sustain reproduction, as observed in the scleractinians (see above). For instance *Primnoa pacifica*,

which can be found from 9–900 m depths (Fig. 4), has been shown to have arrested development of gametes in the shallower, warmer, extent of its range (Waller et al. 2014, 2019; Johnstone et al. 2021).

Pennatulacea

All species of deep-water pennatulaceans examined to date are gonochoric (Fig. 5), and while gametogenesis follows the general model described above (Fig. 6), electron microscopy has been used to further examine gametogenesis. For example, Eckelbarger et al. (1998) studied *Pennatula aculeata* from the Gulf of Maine (USA) and demonstrated that both oocytes and spermatocysts were surrounded by flagellated follicle cells, and gametes were expelled out of the mesenteries into the gastrovascular cavity where they completed their development, presumably fed by the follicle cells (Eckelbarger et al. 1998).

Stylasteridae

There are limited reproduction studies on stylasterids, even those that live in shallow waters. Therefore, patterns are hard to elucidate, particularly when 12 of the 13 specimens of deep-sea stylasterids come from a single sampling period in waters off Alaska, USA (Brooke and Stone 2007). All the deep-sea stylasterid species compiled for this review are gonochoric, and indeed, this is a pattern seen in shallow-water species as well, with just one species to date being recorded as hermaphroditic (Cairns 2011). Stylasterids have three types of polyps, i.e., dactylozooids, gastrozooids, and gonophores, with the latter being where gametes are formed. Unlike other coral taxa, stylasterids have morphological variations in their polyps between males and females. The ampulla is the skeletal encasement of the gonophore and shows varied morphologies between males and females in each species (Cairns 2011). Gametogenesis has not been well documented in deep-water stylasterid species, though several stages of oogenesis and spermatogenesis were observed in specimens from Alaska and found to follow the general pattern observed in other deep-sea coral taxa (Brooke and Stone 2007).

Sexual maturity and fecundity

As with most aspects of deep-sea coral reproduction, very little is known about the onset of sexual maturity, despite this being another important factor in deep-sea coral population dynamics and capacity to recover from disturbances. The sexual maturity of coral is typically described in terms of age or size at first reproduction, either for the whole individual (solitary or colonial) or for a single polyp. It is difficult to generalize maturity age/size for a species, however, due to the inconsistencies seen in the literature in measuring

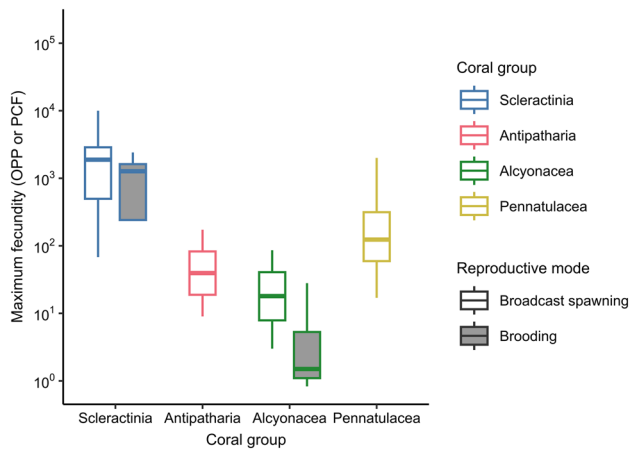


Fig. 7 Fecundity range of deep-sea corals from studies that reported oocyte per polyp (OPP) or potential colony fecundity (PCF), in the case of solitary species, in each taxa, separated by broadcasting (clear) and brooding (shaded) species

these parameters. For example, size at first reproduction may be measured in terms of polyp wet weight, polyp diameter, polyp or colony height, or basal width (Online Resource 1). Reproductive age may, therefore, be more useful for conservation and management applications, particularly in terms of predicting recovery potential. Growth rates, however, can vary between populations inhabiting different habitats or regions, complicating age–maturity relationships (e.g., Choy et al. 2020).

Fecundity estimates are also useful for determining the potential for a species to recover, as this parameter describes the reproductive output, which may be interpreted as a recolonisation potential after a disturbance. Fecundity can, and has been, recorded in several different ways through the published literature (Table 1). These include total number of oocytes per polyp (polyp fecundity); oocytes per unit of area (e.g., 1 cm^2); mature oocytes per polyp (potential relative fecundity); and estimated number of mature oocytes per colony, based on an estimate of the total number of polyps (potential colony fecundity). This variation can make comparative analyses difficult, although the majority of studies in this review use ‘oocytes per polyp’ and ‘potential colony fecundity’ (which have the same meaning across colonial and solitary scleractinian species), or ‘potential relative fecundity’, which presents data on mature oocytes only. The latter metric has value for assessing the number of gametes that may be released in the next spawning event (i.e., most likely to generate offspring), and thus should be presented where possible. Generally, brooding species are predicted to have reduced fecundity relative to broadcasting species likely due to space concerns within the polyp tissues (as

brooded larvae are usually larger than spawned gametes) and this general trend was observed among species reviewed here (Fig. 7).

Scleractinia

Among the deep-sea scleractinians, 8 of 24 species have information relating to the minimum reproductive size, representing five families (Caryophyllidae, Flabellidae, Fungiacyathidae, Oculinidae, and Rhizangiidae). Within family Caryophyllidae, the solitary cup coral *Desmophyllum dianthus* and colonial reef-forming species *Lophelia pertusa** are the only deep-sea species with sexual maturity data. Apparent differences in the approximate maturity size of *D. dianthus* collected from the Patagonian Fjords were found between male and female polyps, with the smallest female reproducing polyps in surface area (150 mm^2) being almost twice the size of the smallest mature male polyps (82 mm^2 ; Feehan et al. 2019). Minimum polyp size for reproduction is generally seen as being larger in the cup corals compared to colonial reef-forming species. For instance, the smallest sexually mature polyp of *Fungiacyathus marenzelleri** had a diameter of 10.0 mm (Waller et al. 2005) compared to *Madrepora oculata*, which were found to have mature polyps with a diameter as small as 1.2 mm (Waller and Tyler 2005). Similarly, the minimum wet weights of reproducing polyps in the solitary flabellid species *Flabellum alabastrum** and *F. angulare** (0.25 and 1.38 g, respectively; Waller and Tyler 2011) were significantly larger than those found for the colonial *L. pertusa** (0.08 g; Waller and Tyler 2005), though the former species have significantly larger polyps. None of the scleractinian studies compiled here estimated age at sexual maturity; therefore, we are unable to reliably determine the time after settlement that these species are capable of sexual reproduction. Given the estimated slow growth rates of deep-sea scleractinians (Roberts et al. 2009), it is likely that they may take at least several years to reach sexual maturity.

Estimates of fecundity were reported for 20 of 24 total scleractinian species included in our review. Polyp fecundity varied greatly between species in order Scleractinia, with the mean number of oocytes per polyp ranging from 10 in *M. oculata* (Waller and Tyler 2005) to over 170,000 in *D. dianthus* (Feehan et al. 2019). Overall, polyp fecundity was generally (though not exclusively) higher in solitary cup coral species than colonial reef-forming species, irrespective of family, likely due to polyp size often being larger in solitary corals. The maximum number of oocytes per polyp observed in most of the included solitary species was nearly one thousand to tens of thousands (Table 1), whereas fecundity of the reef-forming scleractinians was often considerably lower at tens to hundreds of oocytes per polyp. Despite overall differences in polyp fecundity, it is likely that total colony

fecundity is generally higher for colonial species, because these individuals will have many multiples of polyps.

Across all deep-sea Scleractinia species with fecundity data, we found a weak positive correlation between maximum collection depth and maximum polyp fecundity (Online Resource 2). At the family level, a positive correlation between depth and fecundity was observed among species in the families Caryophyllidae and Flabellidae. In contrast, a weak negative correlation between depth and fecundity was observed in species of Fungiacyathidae. While seven deep scleractinian species have been examined from different environments, fecundity was only reported for two and showed differences between populations (Table 1). For *Fungiacyathus marenzelleri**, reported differences were hypothesized to be food related, with deeper populations receiving less food and thus allocating less energy for reproduction (Waller and Feehan 2013).

Antipatharia

Only two species in this review [*Antipathes griggi* (family Antipathidae) and *Antipathella fiordensis* (family Myriopathidae)] have information on size or age of sexual maturity, which was positively correlated with total colony size in both species (Wagner et al. 2012a; Parker et al. 1997).

There has also been little research regarding the fecundity of deep-sea antipatharians: only three species representing two families, Myriopathidae and Schizopathidae, include fecundity estimates. Research done thus far indicates that polyp fecundity is substantially reduced in antipatharians compared to the scleractinians, but similar to estimates obtained for the Alcyonacean species (Fig. 7). Fecundity of *A. fiordensis* sampled from Fiordland (New Zealand) varied between colonies, ranging from 12 to 173 oocytes per polyp; as well as within colonies, with polyps at the bottom of the colony harboring more oocytes than those at the top (Parker et al. 1997). In colonies of *Antipathella wollastoni* collected from shallow depths in the Azores (Portugal), fecundity was found to vary greatly, ranging from 1 to 309 oocytes per polyp (Rakka et al. 2017). A positive correlation between colony height and polyp fecundity was observed in both *A. fiordensis* and *A. wollastoni* (Parker et al. 1997; Rakka et al. 2017), indicating that larger colonies may allocate more energy toward reproductive output than smaller ones. Maximum polyp fecundity was found to be considerably lower in *Dendrobathypathes grandis* than in the other two species with available data (Lauretta and Penchaszadeh 2017).

Alcyonacea

Information on the maturity size/age of the deep-sea alcyonacean corals was obtained for seven species, representing five families (Alcyonidae, Corallidae, Keratoisididae, Primnoidae, and Plexauridae). Within family Alcyonidae, maturity sizes of the gonochoric mushroom coral *Anthomastus grandiflorus* collected in the Northeast Atlantic were found to vary slightly between male and female colonies, with the smallest mature male colonies having average wet weights of 1.5 g compared to 1.7 g in females, and composed of only five polyps (Mercier and Hamel 2011). If growth rates of this species are similar to those estimated for *Anthomastus ritteri** (see Cordes et al. 2001), the minimum mature colony sizes reported by Mercier and Hamel (2011) indicate that *A. grandiflorus* may reach sexual maturity within 3 years of settlement. Consequently, the age at sexual maturity may be substantially lower in the Alcyonidae than in the families Corallidae, Primnoidae, and Plexauridae, which may reduce their vulnerability to fisheries damage (Goode et al. 2020). The estimated ages of first reproduction for the coralliid *Corallium rubrum*, primnoids *Primnoa resedaeformis* and *Primnoa pacifica*, and plexaurid *Paramuricea placomus* were 7, 7.6–19.8, 23–33, and 20.7–37 years, respectively (Torrents et al. 2005; Fountain et al. 2019; Waller et al. 2019). In gonochoric alcyonaceans, the age at first reproduction may be correlated with sex of the colony, whereby males take longer to mature than females (Fountain et al. 2019). Overall, there is still much we do not know regarding how or when deep-sea alcyonaceans become sexually mature.

In total, 22 of 31 alcyonacean species included in our review have fecundity data, representing all eight families examined. Polyp fecundity overall is relatively low compared to the deep-sea scleractinians, antipatharians, and pennatulaceans (Fig. 7), though this difference may be offset by the large number of polyps in branched gorgonians, allowing for high total colony fecundity (Beazley and Kenchington 2012). A positive correlation between coral colony size and polyp fecundity has been observed for several deep-sea alcyonacean species, including the coralliid *C. rubrum* (Torrents et al. 2005; Priori et al. 2013), keratoisid *Acanella arbuscula* (Beazley and Kenchington 2012), and primnoid *P. resedaeformis* (Fountain et al. 2019). This suggests that larger colonies may contribute significantly more to localized reproduction than smaller colonies, but this correlation may weaken once coral colonies reach a certain age (Fountain et al. 2019). In some species, polyp fecundity was also found to vary with the polyp's position along the colony, complicating estimates of total reproductive output. For example, some species have increased fecundity on the distal polyps compared to proximal polyps (e.g., *A. arbuscula*; Beazley and Kenchington 2012), whereas others display the

opposite trend in which polyp fecundity increases toward the center of the colony (e.g., the primnoids *D. acanthina*, *F. rossi*, *F. spinosa*, *Thouarella*, and *A. antarcticum*; Orejas et al. 2007). Fecundity has also been shown to vary within colonies of the same species, which has been attributed to geographical and depth differences (Mercier and Hamel 2011; Fountain et al. 2019; Waller et al. 2019). Orejas et al. (2007) found that fecundity among Antarctic primnoids was similar to those of other octocorals sampled at similar latitudes, and suggested instead that for this group, morphology may be a more important determinant of fecundity than environmental differences. Together these studies of deep-sea alcyonacean reproduction demonstrate the difficulties associated with teasing out the possible causes of intra- and inter-specific variability in polyp fecundity.

Pennatulacea

Sexual maturity data were obtained for four of eight total deep-sea pennatulacean species with reproductive information: *Halipterus finmarchica**, *Anthoptilum grandiflorum*, *Pennatula aculeata*, and *Umbellula encrinus*. Each species represents a different family—Balticinidae, Anthoptillidae, Pennatulidae, and Umbellulidae, respectively—therefore, it was not possible to make intra-family comparisons. The minimum size at first reproduction of *H. finmarchica** collected from the Northwest Atlantic was 18 cm colony length, or 12% of the maximum colony length (Baillon et al. 2015). This proportion is smaller than that observed for the sympatric species *A. grandiflorum* (28%; Baillon et al. 2014b), indicating that *H. finmarchica** reaches maturity at a proportionally smaller size than *A. grandiflorum*. Estimated linear growth rates of *H. finmarchica** (4.3–4.9 cm per year; Neves et al. 2015) suggest that individuals may become reproductive around 3–4 years of age (Baillon et al. 2015). In the boreal/polar species *U. encrinus*, observed sizes at first reproduction of male colonies were smaller (19–33 cm height) than those of female colonies (52–55 cm; Hamel et al. 2020). Given that *U. encrinus* colonies can reach heights over 2 m, males may mature at 7–14% of their maximum colony size and females at 23–24% maximum colony size (Hamel et al. 2020), similar to proportional sizes reported for *H. finmarchica** and *A. grandiflorum*. Estimated linear extension growth rates of *U. encrinus* (mean of 4.5 cm y⁻¹; de Moura Neves et al. 2018) indicate males mature at approximately 4–7 years of age and females at approximately 11–12 years. The currently limited information suggests that deep-sea pennatulaceans generally mature earlier than gorgonian alcyonaceans; however, it remains uncertain how sexual maturity in deep-sea pennatulaceans is correlated with abiotic factors.

Fecundity data were reported for six of the eight pennatulaceans compiled, representing four families (Balticinidae,

Anthoptillidae, Funiculinidae, and Umbellulidae). In the family Umbellulidae, colonies of *U. lindahi* from the Porcupine Seabight (Northeast Atlantic) had substantially greater total polyp fecundity (2000 oocytes per polyp, Tyler et al. 1995) than colonies of the congeneric *U. encrinus* collected in the Canadian Arctic (80–170 oocytes per polyp, Hamel et al. 2020). Polyp fecundity of *U. encrinus* was positively correlated with both colony height and increasing depth (Hamel et al. 2020). Differences in fecundity between *U. encrinus* and *U. lindahi* may be due, at least in part, to different quantification methods; Hamel et al. (2020) reported polyp fecundity as the number of mature oocytes present just before spawning, or effective relative fecundity (ERF), whereas Tyler et al. (1995) reported fecundity as 2000 ‘large’ oocyte per polyp. These differences aside, the Umbellulidae species still seem to have greater polyp fecundity relative to species from other families, including *A. grandiflorum* (6–31 mature oocytes per polyp; Baillon et al. 2014b), *A. murrayi* (90 oocytes per polyp; Pires et al. 2009), and *H. finmarchica** (6 oocytes per polyp; Baillon et al. 2015). Colony fecundity is similar among all the deep-sea pennatulaceans examined to date, and thus, polyp fecundity may be balanced somewhat by the total number of polyps.

Stylasteridae

There are currently no explicit data regarding the sexual maturity or fecundity of deep-sea hydrocorals in the family Stylasteridae, but these species are fast-growing (up to 7 cm per year; Miller et al. 2004) and are therefore hypothesized to rapidly reach sexual maturity relative to the other coral groups examined here. Additionally, because they are relatively small compared to other deep-sea corals and most are known as brooders (Cairns 2011), stylasterid corals are likely to have reduced fecundity compared to alcyonacean, pennatulacean, scleractinian, and antipatharian species.

Reproductive mode and seasonality

Studying seasonal patterns in the reproduction of cold-water and deep-sea corals is challenging both from the perspective of understanding and accurately detecting them. Seasonality is typically defined as a component of a time series that displays repetitive and predictable changes over a period of one calendar year or less. It should be noted that biennial cycles are also possible for species that live in cold environments; as such, periodicity is perhaps a more accurate term than seasonality.

Seasonal or otherwise periodic reproductive cycles in all benthic organisms are more often determined indirectly, by looking at stages of gamete development to infer the time of their maturation and release, than directly by witnessing actual reproductive spawning or offspring release events.

Therefore, our capacity to identify breeding periods relies almost entirely on being able to understand gametogenic (typically oogenetic) patterns. While most studies on reproductive periodicity have focused on gamete development and release, cycles in the release of post-zygotic propagules (e.g., larvae) can also be examined in brooding species. Therefore, in the case of deep-sea corals, one can look at patterns in gametogenesis, spawning events, or planulation pulses and attempt to correlate them with large-scale environmental conditions that define seasons, primarily photoperiod and sea surface temperature, and related differences in food availability (see Giese 1959; Chia et al. 1991; Olive 1995; Himmelman 1999; Mercier and Hamel 2009; Maier et al. 2020). It is widely accepted that periodicities in reproduction (or portions thereof) can either be driven directly by cyclic environmental changes ('environmentally constrained') or involve the action of a biological clock ('phylogenetic constrained') entrained by external stimuli (Eckelbarger and Watling 1995; Mercier and Hamel 2014). For species that live in cold waters, spring and early summer (in either hemisphere) are generally the most intense breeding periods, irrespective of reproductive strategy (broadcast spawning or brooding) and larval type (feeding or non-feeding) (Reitzel et al. 2004; Mercier and Hamel 2010). For instance, seasonal pulses in primary production (phytoplankton blooms) result in subsequent deposition of phytodetritic matter that has long been recognized as a putative driver of periodic/seasonal reproduction (Goody and Turley 1990). An additional layer of complexity in deep-water species comes from the fact that seasonal environmental cues can be delayed or obscured by the depth factor.

There is a high likelihood that the current knowledge is underestimating the proportion of periodical breeders within deep-sea coral taxa. While the adaptive value of reproductive rhythms is well known, gathering evidence of their occurrence for deep-sea species is difficult due to logistical sampling constraints. Live animals can only be observed for brief periods in situ and are rarely held in conditions suitable for long-term study (although there are exceptions). The sporadic and multidisciplinary nature of deep-sea expeditions also means that preserved samples are typically collected across broad temporal and spatial scales (e.g., having to collect over several years to obtain samples from most months or seasons; having to combine samples collected hundreds of kilometers apart). These limitations can prevent the observation of tell-tale peaks corresponding to spawning/planulation events, especially if they are brief and/or restricted to a small proportion of colonies (Baillon et al. 2011). Other potential difficulties in detecting reproductive periodicities include spatial variations in the reproductive status of polyps within an individual: for instance, oocytes developing asynchronously along the different sections of coral colonies,

and the simultaneous development of multiple cohorts of oocytes within polyps or colonies. Overall, complex oogenic patterns, where multiple stages or cohorts of oocytes are detected, can easily lead to assumptions of 'continuous' or aperiodic reproduction, especially when working with few samples that may not have been optimally preserved and do not cover most of one complete or two consecutive annual cycles.

Despite the many constraints, and somewhat contrary to initial assumptions, a good number of the deep-sea coral species that have been investigated so far have been found to display convincing evidence of reproductive periodicity, with examples that include most major groups and span across bathyal and abyssal depths (Table 1). Below is a breakdown of evidence gathered for representatives of the main deep-sea coral taxa examined to date. Unsurprisingly, knowledge of periodicities does not exist for most species. When data are available, support for periodicity is slightly greater, with some of the clearest evidence of reproductive periodicity obtained either from relatively complete time series of samples or from the study of live specimens that underwent successive spawning/planulation events in the laboratory.

Scleractinia

A previous review of reproductive processes among members of the Scleractinia order had concluded that around half the number of species examined exhibited periodicity (Waller 2005). It remains true to date, despite the increased number of examined species, that a roughly equal number of studies on scleractinians have concluded that they undergo periodic versus aperiodic reproduction.

Several colonial forms of deep-sea scleractinians have been investigated using histological techniques. Among them, *Lophelia pertusa** and *Madrepora oculata* sampled from the Porcupine Seabight exhibited differences, with the former having seasonal reproduction and the latter displaying equivocal results suggesting multiple cohorts of gamete production with undetermined periodicity (Waller and Tyler 2005). Three species of solitary corals in the *Caryophyllia* genus (*C. ambrosia*, *C. cornuformis**, and *C. sequenzae*) collected from the two same sites were found to be hermaphroditic and their gametogenic cycle did not show any evidence of periodicity (Waller et al. 2005). In contrast, three gonochoric species of reef-forming corals occurring in New Zealand waters (*Goniocorella dumosa*, *Solenosmilia variabilis*, and *Enallopsammia rostrata*) were estimated to undergo external fertilization in late April or May coinciding with pelagic biomass accumulations at the end of summer (Burgess and Babcock 2005, though see Tracey et al. (2021)

for *G. dumosa*). The investigators found that gametogenesis displayed a high level of synchrony among species and between the seamount localities on which the samples were taken.

In solitary forms of the genus *Flabellum*, reproductive modes were found to vary between different habitats: *Flabellum* spp. collected from the Northwest Atlantic was determined to freely release gametes (Mercier et al. 2011; Waller and Tyler 2011), whereas those on the continental shelf of the Western Antarctic Peninsula were determined to brood until the planula larval stage (Waller et al. 2008). The difference in feeding modes between *Flabellum* species has been proposed in global studies as a potential reason for variation in reproductive periodicity (e.g., aperiodic versus seasonal spawners). For example, spawning of *F. angulare** in the Northeast Atlantic may be restricted to late summer during seasonal phytoplankton blooms in this region due to a more restricted diet compared to the carnivorous or mixed diet of *F. alabastrum**, which reproduces without any clear periodicity (Waller and Tyler 2011). In another genus of solitary coral (*Fungiacyathus marenzelleri**) sampled in the Northeast Atlantic, overlapping gametogenic cycles were histologically determined to occur in both sexes and there was a non-significant trend toward a synchronous spawning event in summer (Waller et al. 2002). In recent years, investigators have become more cautious in making diagnostics based on low sample sizes. For example, individuals of the cup coral *Balanophyllia malouinensis* sampled from sub-Antarctic regions displayed spermatocysts and oocytes at varying stages of development, but investigators concluded that periodicity could not be confidently determined (Pendleton et al. 2021). Some studies have been conducted on shallow-water representatives of deep-water species. For instance, individuals of *Desmophyllum dianthus*, a cosmopolitan species usually found at 1000–2500 m depths, were sampled at 8 m in a Patagonian fjord and determined to be highly seasonal in their gametogenic development, and presumably in their broadcast spawning (Feehan et al. 2019).

Antipatharia

Most antipatharian species (black corals) are hypothesized to freely spawn their gametes (Wagner et al. 2011) and only three have been explicitly examined for evidence of breeding periodicity. *Antipathella fiordensis* and *A. wollastoni* from the Azores (Portugal) in the Atlantic, and *Antipathes griggi* from Hawaii (USA) in the Pacific have all been hypothesized to undergo seasonal reproduction coinciding with increased sea surface temperatures during late summer or fall, respectively (Miller 1996; Wagner et al. 2012a; Rakka et al. 2017). We note that care should be taken to ensure that hemisphere is considered when ‘seasons’ are reported.

Alyconacea

Among alcyonaceans, research has been completed on a number of the skeleton-forming species (gorgonian octocorals) and most species for which the reproductive cycle was examined display some form of periodicity. Members of the family Primnoidae (*Fannyella rossii*, *F. spinosa*, and *Thouarella* sp.) were found in an Antarctic study to display overlapping gamete generations taking more than 1 year to develop. In particular, *F. rossii* and *F. spinosa* showed only one size class of oocytes, possibly indicative of annual broadcast spawning, whereas the presence of larvae in the gastrovascular cavities in both *Fannyella* spp. and *Thouarella* sp. was proposed to indicate larval release during austral summer (Orejas et al. 2007). Clear evidence of seasonal broadcast spawning was also provided for the keratoisid species *Keratoisis ornata**, in which spawning likely occurs in late summer/fall to coincide with increased seawater temperature and detrital post-bloom deposition on the eastern Canadian seaboard (Mercier and Hamel 2011). In contrast, in a nearby region of the Northwest Atlantic, a member of the same family (*Acanella arbuscula*) did not display any evidence for seasonal reproduction, nor did the primnoid *Primnoa resedaeformis* (Beazley and Kenchington 2012), which could be due to limited temporal sampling and/or environmental differences, such as depth and food availability (Mercier and Hamel 2011; Beazley and Kenchington 2012). Another primnoid sampled in Alaskan (USA) waters (*P. pacifica*) displayed oocyte development that spanned more than a year and was suggested to undergo asynchronous and aperiodic spawning, possibly split into two-to-three annual events (Waller et al. 2014, though see Johnstone et al. 2021). Two deep-sea corals in the family Coralliidae studied in Hawaii (USA), *Corallium laauense** and *C. secundum**, were similarly predicted to broadcast spawn without any clear periodicity, based on the simultaneous presence in the polyps of oocytes and spermatocysts at various stages of maturity (Waller and Baco 2007). A comparable diagnostic was made for *Dentomuricea* aff. *meteor* (Plexauridae) and *Viminella flagellum** (Ellisellidae) from the Azores, because female colonies displayed oocytes throughout the study period and their size distributions displayed no evidence of seasonality (Rakka et al. 2021a,b). Importantly, species that appear to undergo aperiodic or ‘continuous’ production of gametes may still be influenced by environmental cues to release mature gametes on an opportunistic or rhythmic basis aligned with optimal conditions (Mercier and Hamel 2011).

Another group of alcyonaceans, those in the family Nephtheidae (‘true soft corals’), have largely been shown to brood larvae and undergo seasonal reproduction (planulation peaks) in the Northwest Atlantic. In *Drifa glomerata* and *Drifa*

sp., larval release in live colonies kept under flow-through laboratory conditions closely followed predictions based on the examination of field samples (Sun et al. 2010a, b). Data showed that larval production seemed to persist year-round, yet the onset of major planulation events was seasonal over two consecutive years, one peak coinciding with an increase in photoperiod and peak temperatures at 150 m, and a second peak following the phytoplankton bloom (Sun et al. 2010a). Interestingly, *Drifa* species are known to possess distinct reproductive polyps (Sun et al. 2009) and their planulation pulses were found to exhibit clear lunar components during the reproductive season (Sun et al. 2009, 2010a, b; Mercier and Hamel 2014). Another brooding nephtheid from the same ocean basin was determined to undergo seasonal breeding in mesocosms; peak planulation in *Gersemia fruticosa* coincided with high levels of chlorophyll concentration and deposition of planktic matter (Sun et al. 2011).

Pennatulacea

Among deep-sea pennatulaceans, seasonal reproduction appears to be the dominant pattern. It has been determined to occur in three species from the Northwest Atlantic, *Anthoptilum grandiflorum* (Baillon et al. 2014b), *Halipteris finmarchica** (Baillon et al. 2015), and *Pennatula aculeata* (Couillard et al. 2021). Interestingly, both *H. finmarchica** and *P. aculeata* were found to need more than a year to produce mature oocytes, indicating that given females may only spawn on a biennial cycle, while annual spawning would occur at the population level (Baillon et al. 2015; Couillard et al. 2021). Another species of *Anthoptilum* (*A. murrayi*) sampled off Brazil in the southwestern Atlantic at 1300–1800 m displayed no clear evidence of a seasonal reproductive pattern according to the investigators (Pires et al. 2009). In *Umbellula encrinus* collected at bathyal depths in Baffin Bay (N. Atlantic Sub Arctic, Fig. 1), gametogenesis was synchronous between sexes and appeared to be completed over a single annual reproductive cycle, with spawning possibly occurring in summer, following the disappearance of the ice cover and the increase in chlorophyll-a (Hamel et al. 2020). At the southern pole, the reproductive ecology of the pennatulid *Malacobelemnion daytoni* was studied using monthly samples over a 2-year period. Immature oocytes and spermatocytes were present year-round, but maturation was seasonal; thus, it was proposed that multiple spawning events could occur per year, driven by the presence of suspended particulate matter (Servetto and Sahade 2016).

Stylasteridae

There are no known data on periodicity or seasonality in the deep-water stylasterids to date. Of the few studies available

on this group, most species are either confirmed or predicted to brood their larvae, whereas the reproductive strategy in others remains unknown (Miller et al. 2004; Brooke and Stone 2007); hence, brooding until the larval stage is hypothesized to be the only reproductive mode in the Stylasteridae (Cairns 2011).

Fertilization, larval formation, and settling

Though very little is known, recent work has greatly added to the understanding of the early life history of deep-sea corals and additional descriptions are forthcoming. Unlike periodicity or seasonality, which can be inferred to some extent from the condition of unreleased gametes, understanding fertilization dynamics is especially challenging, requiring precisely timed observations either in situ or in reproductive populations maintained in the laboratory. For many deep-sea coral species, information essential for planning expeditions to observe in situ fertilization, such as reproductive mode and phenology, remains unknown. Even for species where that is known, the rapid nature of fertilization makes the chance of observation extremely low. As a result, there are no detailed descriptions of fertilization dynamics in deep-sea corals to date. There are, however, a small number of species for which laboratory-held populations have supported useful descriptions of spawning behavior and initial observations of sperm–egg interactions (e.g., Heltzel and Babcock 2002; Larsson et al. 2014). For some of these species, efforts to characterize classical aspects of fertilization such as spermatozoa swimming speed, gamete longevity, and optimum fertilization curves are ongoing. Based on inferences from reproductive mode and related shallow-water species, fertilization in deep-sea corals is thought to occur internally in brooding species and externally in broadcast spawners and surface-brooders.

The products of successful fertilization, larvae, are also challenging to study in situ, because they are only present ephemerally and are small and dispersive by nature. Again, live, laboratory-held samples have provided a unique opportunity to study the early life histories of several deep-sea coral species. Such investigations have capitalized on species that survive well in captivity, occur in areas of accessible depths, have suitable sample availability, or have known spawning seasons (Szmant-Froelich et al. 1980; Tranter et al. 1982; Cordes et al. 2001; Heltzel and Babcock 2002; Altieri 2003; Brooke and Young 2003, 2005; Mercier et al. 2011; Sun et al. 2010a,b, 2011; Larsson et al. 2014; Strömberg and Larsson 2017; Rakka et al. 2021a,b; Heran et al. 2023; Tracey et al. 2021; Johnstone et al. 2022). Additionally, preserved specimens can, in some cases, be used to describe brooded larvae in instances where developing larvae have been preserved within the parent polyp (Waller et al. 2008;

Goffredo et al. 2012; Pendleton et al. 2021). Another clue to larval formation that may be gleaned from preserved samples is the mode of larval nutrition. Using oocyte size and lipid content, it is possible to suggest a lecithotrophic (sustained by yolk reserves) or planktotrophic (feeding on plankton) larval diet, which, in turn, has implications for larval behavior; however, this method is not always an accurate predictor (e.g., Strömberg and Larsson 2017).

Larval development is crucial to understanding the health and connectivity of deep-sea coral populations, because it is directly related to a species' dispersal capability. Pelagic larvae can take advantage of currents to disperse far beyond their natal habitat, while crawling larvae are thought to be much more limited, often dispersing only a few meters from their parent polyp/colony. In both cases, learning about larval longevity, precompetency period length, and settlement preferences are key inputs to models of larval dispersal and population connectivity (Holland et al. 2022). Patterns of larval development in deep-sea species do appear to follow those described for other anthozoan species thus far (Hyman 1940; Martin 1997). The embryo proceeds through blastulation, gastrulation, and ultimately becomes a planula larva. The larva then swims or crawls to find a suitable location to settle (Hyman 1940; Martin 1997). Caution should be taken in applying this general pattern to deep-sea corals, as the number of species examined is low, and anthozoans are known to vary widely in their developmental processes, and the few model species whose development has been thoroughly described are shallow tropical species.

A summary of the current state of knowledge of deep-sea coral larval biology follows. It should be emphasized that these studies may not reflect widespread trends, as not all groups are represented and this representation is not evenly distributed. For example, while there have been relatively thorough descriptions of larval development based on direct observation in some species of scleractinians and alcyonaceans, there are no existing studies in stylasterid or antipatharian species. Given this, and the known variability of larval development pathways in Anthozoa broadly, the data summarized below should only be considered an initial survey of larval development in cold-water corals.

Scleractinia

The order Scleractinia includes some of the most thoroughly studied species of deep-sea coral in terms of larval development. Larval stages of twelve species of Scleractinia have been described, representing five families. The reports of larvae in this order cover both pelagic and demersal larval forms, hypothesize examples of internal and external fertilization, and have settlement periods ranging from several days post-release (*Goniocorella dumosa*, Tracey et al. 2021;

Balanophyllia elegans, Altieri 2003) to over 50 days (*Lophelia pertusa**, Strömberg and Larsson 2017).

In the family Caryophylliidae, larval characteristics have been described for five species. Among the genus *Caryophyllia*, *C. huinayensis* and *C. smithii* produce active, swimming larvae; however, the mode of locomotion is unknown for *C. inornata*, in which brooded embryos ultimately develop a mouth, pharynx, and gastrovascular cavity prior to release (Tranter et al. 1982; Goffredo et al. 2012, Heran et al. 2023). In *Lophelia pertusa**, larvae develop to fully ciliated planulae within 2 weeks of fertilization, with early cleavages occurring every 6–8 h and indications of gastrulation appearing 6 to 8 days post-fertilization (Larsson et al. 2014). The larvae of *L. pertusa** have the potential for long-distance dispersal given their longevity and behavior in the laboratory, migrating upwards for the first 5 weeks, then shifting to a primarily downward migration (Strömberg and Larsson 2017). During experiments to simulate these vertical migrations, larvae of *L. pertusa** crossed salinity gradients and withstood lower salinities (~25 psu), indicating that they may reside in the faster-moving currents of the photic zone for some of their pelagic phase (Strömberg and Larsson 2017). A southern hemisphere reef builder, *Goniocorella dumosa*, was once thought to be a broadcasting species (Burgess and Babcock 2005), has now been discovered to brood actively swimming larvae that settle within 2–8 days of release in aquaria (Tracey et al. 2021). Indeed, this species highlights the need for greater resolution in seasonal sampling; otherwise, crucial information, such as broadcasting or brooding, could be missed.

In *Balanophyllia elegans* (Dendrophyllidae) larvae crawl to find a suitable place to settle within 1 m of their parent, recruiting to the substrate after 48 h (Altieri 2003). Interestingly, evidence from Altieri (2003) suggests that water flow and substrate availability were important for successful settlement in this species. Several deep-living members of the family Flabellidae that have been investigated were found to internally brood their larvae (*Flabellum curvatum*, *F. impensum*, *F. thouarsii*, and *Monomyces rubrum*). Upon release, these larvae crawl along the substrate to a settlement location likely within a short distance from their parent (Heltzel and Babcock 2002; Waller et al. 2008; Fig. 8). Larval development is not strictly synchronized in these species; even in *M. rubrum*, the species with the most evidence for reproductive periodicity of the four. In *M. rubrum*, larvae are released on a semi-lunar schedule over 3 months (Heltzel and Babcock 2002). In *F. impensum* and *F. curvatum*, two planular stages were observed in brooded offspring, while in *F. thouarsii*, a third, elongate stage was involved (Waller et al. 2008, Fig. 8). In *F. thouarsii*, some stage of developing larvae was always present within female mesenteries (Waller et al. 2008). Larvae of *F. impensum* settle within 7 days of



Fig. 8 Larval stages of two Antarctic scleractinian species, *Flabellum impensum* (top) and *F. thoursii* (bottom). Development is shown from left to right, from immature to settlement. Scale bar = ~1 mm. Composite courtesy of R. Waller

release and have exhibited resilience to increased temperatures during development (Johnstone et al. 2022). Larvae of another Flabellidae member, *F. angulare**, are not brooded, but rather the result of oocytes released in tethered bundles of 3–5 and fertilized externally (Mercier et al. 2011), showing similarities to surface brooding described for some shallow species of octocorals (see Kahng et al. 2011). After an initial period of retention on the tentacles of the spawning parent, embryos either fell to the substrate or floated to the surface, developing into planula larvae within 24 h (Mercier et al. 2011).

Oculina varicosa, the single deep-sea representative of the family Oculinidae whose larvae have been studied, was found to produce planktotrophic larvae that swam actively for 1–2 weeks, then began probing the substrate after 10–14 days, ultimately settling and metamorphosing after 21 days (Brooke and Young 2003, 2005). In *Astrangia danae**, of the family Rhizangiidae, ciliated larvae developed quickly, relative to other deep-sea corals, becoming phototactic, ciliated gastrulae within 6–8 h of fertilization, and presenting as a fully developed, elongated planula with a mouth and pharynx after 36 h (Szmant-Froelich et al. 1980). These larvae were observed to swim at the water surface for 12–15 h after fertilization, switching to near bottom or midwater swimming after 48–72 h post-fertilization as their attraction to light appeared to lessen (Szmant-Froelich et al. 1980).

Antipatharia

Very little data exist on the larvae of antipatharian species, but the shallower-living *Antipathella fiordensis* is one exception. This species has been shown to produce lecithotrophic crawling larvae that are likely to have limited potential for

dispersal, matching this species very limited distribution (Miller 1996, 1997, 1998).

Alyconacea

Of deep-sea corals in the order Alcyonacea, the larvae of six species have been described. Most are members of the family Nephtheidae (*Drifa* sp., *D. glomerata*, *Duva florida*, and *Gersemia fruticosa*), but one species belongs to the family Alcyoniidae (*Anthomastus ritteri**) and another to the family Plexauridae (*Dentomuricea* aff. *meteor*). Most of the species studied so far are brooders with crawling, lecithotrophic larvae (*Drifa* sp. and *D. glomerata*, Sun et al. 2010a; *D. florida*, Sun et al. 2011; *A. ritteri**, Cordes et al. 2001), although one produced swimming larvae (*G. fruticosa*, Sun et al. 2011), and *Dentomuricea* aff. *meteor* is a broadcast spawner (Rakka et al. 2021a). Generally, in the species studied to date, settlement occurs within a few days of larval release (*Drifa* sp. and *D. glomerata*, Sun et al. 2010a; *A. ritteri**, Cordes et al. 2001), but may be delayed up to several weeks (*D. florida* and *G. fruticosa*, Sun et al. 2011; *D. aff. meteor*, Rakka et al. 2021a). Among the studied species, settlement preferences seem to be variable: in some investigations, larvae preferentially settled on preconditioned, rough surfaces (*Drifa* sp. and *D. glomerata*, Sun et al. 2010a), whereas in other cases, larvae avoided such surfaces in favor of the smooth sides of the culture vessel (*D. aff. meteor*, Rakka et al. 2021a).

The species *Anthomastus ritteri**, of the family Alcyoniidae, produces internally fertilized embryos and larvae that crawl by ciliary action or are transported passively by water movements until settling after about 48 h (Cordes et al. 2001). Metamorphosis takes place within approximately 6–7 days, indicated by the development of tentacle buds

and permanent attachment to the substrate (Cordes et al. 2001). Most larvae follow this timeline; however, some may take substantially longer to settle, reportedly up to 123 days (Cordes et al. 2001). Surface brooding, whereby oocytes are fertilized (either internally or externally) and incubated outside the polyp, has been described for shallow species of alcyonaceans (see Kahng et al. 2011) and suspected for *Primnoa pacifica* (Waller et al. 2014), but it is a method of fertilization that has yet to be conclusively observed in any deep-water species.

Larvae from the family Nephtheidae share some common characteristics, such as their mode of locomotion. Each of these species produces a crawling, demersal larva (Sun et al. 2010a, b, 2011) but while that of *Drifa glomerata* immediately starts probing the bottom with the aboral end from an anchored oral end, the larva of *Drifa* sp. takes longer to settle, using its body shape to change position in the water column (Sun et al. 2010a, b). Larvae of *Duva florida* are also demersal, ciliated crawling planulae; however, rather than performing complex crawling movements or actively managing their position in the water column, they are negatively buoyant and were observed aggregating at the bottom of the culture vessel (Sun et al. 2011). Larvae of *D. florida* began to settle 5 days after being extracted, while *Gersemia fruticosa* settled between 3 and 70 days after release, and this settlement generally coincided with metamorphosis (Sun et al. 2011). The larvae moved between the water column and the benthos, eventually sinking to probe the bottom as described in *Drifa* sp. (Sun et al. 2010a, 2011).

The only species of deep-sea coral from the family Plexauridae whose larvae have been described is *Dentomuricea* aff. *meteor*. Within 4 days, the larvae of this species grow into fully ciliated planula larvae that are negatively buoyant and elongate over time (Rakka et al. 2021a). Although these larvae are capable of swimming, they have only been observed to swim under mechanical stimulation (Rakka et al. 2021a).

Interestingly, larvae of both *Drifa glomerata* and *Dentomuricea* aff. *meteor* were found to metamorphose in the water column (Sun et al. 2010b; Rakka et al. 2021a), suggesting that this ability to ‘pre-metamorphose’ prior to settling may be shared among other species across families. An alternative or complementary cause for these premature metamorphoses is the “desperate larvae hypothesis” (Gibson 1995; Marshall and Keough 2003) whereby larvae can delay settlement until a threshold is reached, potentially related to energetic reserves (Wendt 2000; Elkin and Marshall 2007). Both of these species are lecithotrophic, so in theory after using up some proportion of their lipid-rich yolk, larvae must metamorphose to begin feeding, settled or not.

Pennatulacea

Only one study has documented the larval phase of a deep-water pennatulacean. This single study found that *Ptilosarcus (Leioptilus) guernei*, a broadcast spawning species, produces swimming, lecithotrophic planula larvae capable of settlement within 1 week if appropriate substrates were available, but which could delay settlement at least 30 days absent such substrate (Chia and Crawford 1973).

Stylasteridae

Although very few data exist on the larval development of deep-sea stylasterid corals, they are hypothesized to produce brooded crawling larvae that may therefore settle near their parent (Cairns 2011). In *Errina novaezelandiae*, brooded larvae have been observed to crawl on the surface of the parent colony before dropping to the substrate and finding a location to settle (Miller et al. 2004).

Conclusions and recommendations

This review highlights several potential patterns in the reproduction of deep-sea corals. Gonochorism appears to be the dominant sexual system among deep-sea taxa, and data on sexual maturity and fecundity suggest that most deep-sea anthozoans may take several years to decades to become reproductive, but stylasterids are likely to mature more rapidly. Most species examined were predicted to broadcast spawn, though brooding was observed in several scleractinians, alcyonaceans, and stylasterids. It is likely that asexual modes of reproduction are also important to the maintenance of some species populations; however, this mode is perhaps underrepresented currently because of a dearth of live coral observations. Similarly, many species were thought to exhibit aperiodic spawning, but this may also be an artifact of sampling paucity rather than indicative of reality. A few studies examining larvae to date have shown that many of these species may produce larvae that remain viable for weeks to months, supporting predictions that some broadly distributed species have high dispersal capacity. Of the publications used for this study, however, roughly half involved species with demersal larvae, including some species with occurrences in multiple oceanic basins (e.g., *Monomyces rubrum* is found in both the Pacific and Indian Oceans and *Flabellum impensum* has been recorded crossing the Drake passage and into the South Pacific). It will be interesting to see whether these apparent patterns remain as we continue to accumulate reproductive information on deep-sea coral species, particularly in tandem with genetic information on population connectivity throughout species ranges.

Despite the significant increase in research on deep-sea coral reproduction in the last 20 years (Fig. 3B), less than 7% of any deep coral taxa have had any aspect of reproduction reported (Fig. 3A). While it is encouraging that reproductive research on alcyonaceans looks ready to outpace scleractinians in the near future, the Alcyonacea is more speciose, meaning that the overall percentages of reproductive studies are similarly low at 3.1% and 3.5%, respectively. Thus, we are still at a disadvantage in understanding true reproductive patterns and processes, particularly when compared to the roughly 50% of shallow zooxanthellate scleractinian species that have had aspects of reproduction reported (Harrison 2011). In addition, for most species examined here, there was a low degree of temporal and spatial coverage, making it difficult to determine whether reported observations are representative of the entire species or due to the environmental conditions at the time and location of sampling. Many species have near global distributions and reproductive processes and timing can vary considerably between populations separated by distance, environmental variables, and/or depth (Mercier et al. 2011; Brooke and Järnegen 2013; Waller and Feehan 2013; Pires et al. 2014; Waller et al. 2019; Johnstone et al. 2021).

This paucity of studies no doubt comes from the unique challenges of studying the deep sea. This can be observed in the considerable variation in the amount of data reported in each category we examined (Table 1; Online Resource 1), with exceptionally few species having all reproductive aspects explored across the reviewed studies. Acquiring reproductive data in the deep sea poses significant logistical challenges, from obtaining seasonal samples from remote and weather-dependent areas to sampling corals of sufficient quality and quantity, and so, this lack of comprehensive and/or repetitive studies is not surprising. Examining reproduction, however, is an iterative process, where more complex studies can build from early reproductive assessments (*Lophelia pertusa** being an excellent example, Waller et al. 2005, Brooke and Järnegen 2013, Larsson et al. 2014, Strömberg and Larsson 2017). Therefore, both simplistic early assessments and continued examination of species are encouraged, particularly where the species play an important ecological role for other taxa or represent a poorly understood group. Of particular note across all taxa is the paucity of seasonal studies, and although these data are especially challenging to collect, such work is essential to produce accurate information on reproductive strategies, and along with other biological information, reproductive traits help evaluate aspects of susceptibility and productivity of corals to inform in risk-assessment modeling (Clark et al. 2021). Increased effort could also be made to determine reproductive periodicity, as these data are of importance to spawning, larval studies, dispersal modeling, as well as for conservation measures. Similarly, we note that reproductive

variables were not always collected in a comparable manner due to differing preservation or analysis techniques (Table 1). The development of new preservation (i.e., less toxic) and analytical methods is encouraged, but it should be noted that for reproductive information to be of the most use to the community, comparisons between species and/or populations could be made with reference to potential methodological differences. Furthermore, any deviations from established protocols should be easily identified in publications, along with the benefits of such procedures.

Overall, reproduction and larval dispersal are sensitive yet fundamental ecological processes, critical for sustaining and maintaining populations. Deep-sea corals play an important ecological role in deep ocean environments globally, and thus, understanding their reproductive ecology, and general life histories, is key to understanding the health and potential longevity of these ecosystems in response to our changing planet and ever-increasing anthropogenic pressures. The authors of this review anticipate a sustained pace of exploration and discovery on reproductive traits for these key coral taxa.

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Data/code availability All data generated or analysed during this study are included in this published article (and its supplementary information files).

Declarations

Conflict of interest No authors have a conflict of interest with this review article.

Ethical approval N/A.

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