

# Deep-water Scleractinia (Cnidaria: Anthozoa): current knowledge of reproductive processes

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**Abstract.** Little is known of the basic biology and ecology of the numerous species of deep-water scleractinians found in all the world's oceans. Of all the biological processes, reproduction is the most fundamental. Without knowledge of a species' reproduction, we know little about how they survive both the environment that is the deep-sea, and the increasing anthropogenic effects of man's exploration for new fisheries and energy reserves.

This review collates current knowledge of the reproductive processes of deep-water scleractinians. Only fifteen deep-water species as yet have had their reproduction described in the literature. Gametogenesis, reproductive seasonality and larval ecology are summarised and compared briefly to shallow-water counterparts.

A summary table of all deep-water scleractinian species, for which the reproductive strategy is known, and their sample locations, is presented here. It is hoped this knowledge will be used as a basis for further understanding of how the deep-sea species of this order survive and disperse. These data are also directly applicable to the conservation and management of these deep-sea ecosystems.

**Keywords.** Azooxanthellate Scleractinia, deep-sea, gametogenesis, larval ecology

## Introduction

The presence of scleractinian corals living at depths beyond 100 m has been known for many decades, and yet there is still a paucity of information on their basic biology and ecology. In recent years the ecological value of deep-water scleractinians has become more apparent. Reef building species, similar to those found in shallow-water systems, form important habitats, creating oases on continental shelves and slopes, seamounts and ridges. These habitats support a wide diversity of life. Koslow and Gowlett-Jones (1998) observed 242 species of invertebrates and 37 species of fish associated with *Solenosmilia variabilis* reefs on the Tasmanian Seamounts, whilst *Lophelia pertusa* reefs in the NE Atlantic have been shown to support over 1300 species of associated fauna (ACES 2003). In

addition, over 350 species of invertebrates were collected from *Oculina varicosa* bioherms off the Florida continental shelf (Reed 1992; Koenig et al. 2000).

Of more economic importance to man, many commercial species of fish have been found using these reefs for feeding, protection and reproduction (Koslow and Gowlett-Jones 1998; Rogers 1999; Mortensen 2000). Of particular importance are Orange Roughy, Roundnose Grenadier (Rogers 1999; Mortensen 2000), Gag and Scamp grouper (Brooke and Young 2003) whilst many other fisheries species have also been observed using these reefs (Koenig et al. 2000; Reed 2002).

As traditional pelagic and shallow-water fisheries decline, more fishermen are using deep-water benthic trawls to maintain catches. Large deep-water demersal trawlers now operate in areas of high fish densities, which are often related to coral structures (Wheeler et al. in press). Deep-water reefs were avoided in the past by fishermen because of the damage they caused to expensive nets. However, with developments in equipment, such as rockhoppers and stronger nets, more fishermen are realising the potential of these areas as lucrative fisheries (Koslow et al. 2000; Hall-Spencer et al. 2003). The damage to deep-water coral ecosystems from trawls has been recently observed in many areas around the globe (Probert et al. 1997; Koslow and Gowlett-Jones 1998; Bett 2001; Brooke 2002; Hall-Spencer et al. 2003; Wheeler et al. in press). The Orange Roughy fishery is a classic example. This fish species is found in close association with Tasmanian seamount coral communities, and exploitation has already caused the mass destruction of large reef areas (Koslow and Gowlett-Jones 1998). Within the European margin there has also been active destruction by trawlers occurring within the Darwin Mounds (Wheeler et al. in press). These authors report 28 trawl scars observed in a 5 km<sup>2</sup> area of seabed, and many damaged coral mounds.

As well as fishing pressures, deep-water reefs are also potentially under threat from oil and mineral exploration (Rogers 1999; Bett 2001). Such activities have the potential to cause excessive sedimentation from drilling mud, as well as the production of poisonous chemicals, although no active extraction is occurring at present (Rogers 1999). Only recently have studies targeted the potential impacts of man's various activities on deep-water fauna (Olsgard and Gray 1995; Probert et al. 1997; Jennings and Kaiser 1998; Rogers 1999; Hall-Spencer et al. 2003).

Understanding reproductive processes is essential to aiding conservation and management practices. Reproductive seasonality, gamete quality, fecundity and larval supply of habitat-forming organisms are vital to understanding both ecosystem function and recovery potential following a damaging event. This review presents a summary of the limited information on these basic biological processes in both reef-building and solitary deep-water scleractinians.

## Methods

This review is a synthesis of known research on the reproductive processes of deep-water scleractinians. Information was gathered from both published literature and personal communication from colleagues, and is summarised in Table 1.

## Sexuality

It is generally not possible to distinguish the sex of individual scleractinian polyps or colonies from external morphology. In a few shallow-water hermatypic species, eggs and sperm are different colours, and so may be distinguished in the polyps just prior to spawning (Fadlallah 1983). After fixation and decalcification, ripe oocytes may be observed within the mesenteries if they are large in size (Brooke 2002; Waller 2003).

The majority of shallow-water scleractinians are hermaphroditic (Fadlallah 1983; Richmond and Hunter 1990). Of the deep-water scleractinians studied to date, only three species were observed to be hermaphroditic. These are solitary corals, all species of the genus *Caryophyllia* (Waller et al. in press). All three species show a novel form of hermaphroditism, cyclical sexuality. Here the spermacysts and oocytes develop within the same mesentery, in a continuous cycle, but not synchronously between individuals. Only sperm or eggs are released at any one time, thus preventing self-fertilisation. Both sperm and eggs would therefore be present near-continually in the water column, whereas gonochorism would require ripe males and females to spawn synchronously to ensure fertilisation.

Twelve of the fifteen species of deep-water scleractinian examined to date are gonochoric (Table 1) compared to 75 % of the shallow species known being hermaphroditic (Fadlallah 1983). Gonochorism has been proposed as a more primitive adaptation than hermaphroditism (Goffredo et al. 2000), and may be more important for maintaining genetic diversity (Szmant 1986).

## Gametogenesis

Scleractinians do not have 'gonads' in the traditional metazoan sense of the term. Sperm develop in cysts held together by a mesogleal envelope, hence the term spermacysts. Oocytes develop singularly, but are often found in groups or 'pockets', though there is no direct connection between them.

In shallow-water species, several authors have noted that germ cells are most likely to originate from interstitial cells near the septal filaments (lamellae) (Rinkevich and Loya 1979; Szmant-Froelich 1980; Delvoye 1982; Fadlallah 1983), but there are no data as yet for deep-water species. Gametes of many deep-water species reported appear to develop in the lamellae of the mesentery, eventually migrating into the mesoglea (Brooke 2002; Waller et al. 2002, in press; Waller 2003). Oogonia in *Lophelia pertusa* and *Madrepora oculata* have been observed still attached to the lamellae (Waller and Tyler in press), and even some larger vitellogenic oocytes appear to have a form of attachment (Waller 2003).

Stages of oogenesis in deep-water species studied appear to follow those of shallow-water species (*sensu* Fadlallah 1983). The first stage consists of oogonia attached to the lamellae. These grow into previtellogenic oocytes and migrate into the mesoglea of the mesentery. Previtellogenic oocytes then accumulate large quantities of lipid-rich yolk and form vitellogenic oocytes. The final stage is late vitellogenesis, where a thick cortical granular layer is formed on the outside of the oocyte, prior to release.

**Table 1** Reproductive data known for deep-water scleractinian species

Species	Area	Depth [m]	Sex	Max Oocyte	Fecundity
<i>Fungiacyathus marenzelleri</i> (Vaughan, 1906)	Rockall Trough	2000	Gonochoric	750 µm	2900 opp
<i>F. marenzelleri</i>	California	4100	Gonochoric	750 µm	1290 opp
<i>Lophelia pertusa</i> (Linnaeus, 1758)	Porcupine Seabight	900	Gonochoric	140 µm	3146 opp / 3327 ocm <sup>2</sup>
<i>L. pertusa</i>	Trondheim Fjord	147	Gonochoric	60 µm (mean)	
<i>Madrepora oculata</i> Linnaeus, 1758	Porcupine Seabight	900	Gonochoric	350 µm	10 opp / 256 ocm <sup>2</sup>
<i>M. oculata</i>	Chatham Rise	800-1000	Gonochoric		
<i>Caryophyllia cornuiformis</i> Pourtales, 1868	Porcupine Seabight	435-2000	Hermaphrodite (cyclical)	340 µm	-
<i>Caryophyllia ambrosia</i> Alcock 1898	Porcupine Seabight	1100-3000	Hermaphrodite (cyclical)	630 µm	2900 opp
<i>Caryophyllia seguenzae</i> Duncan, 1873	Porcupine Seabight	960-1900	Hermaphrodite (cyclical)	450 µm	940 opp
<i>Oculina varicosa</i> Lesueur, 1821	Florida	3-100	Gonochoric	100 µm	2115-4693 ocm <sup>2</sup>
<i>Flabellum alabastrum</i> Moseley, 1876	Porcupine Seabight	1800-2250	Gonochoric	1010 µm	~550 opp
<i>Flabellum angulare</i> Moseley, 1876	Porcupine Seabight	1647-2875	Gonochoric	814 µm	~2800 opp
<i>Enallopsammia rostrata</i> (De Pourtales, 1878)	Chatham Rise	800-1000	Gonochoric	400 µm	144 opp
<i>Solenosmilia variabilis</i> Duncan, 1873	Chatham Rise	800-1000	Gonochoric	165 µm	290 opp
<i>Goniocorella dumosa</i> (Alcock, 1902)	Chatham Rise	800-1000	Gonochoric	135 µm	480 opp
<i>Flabellum thoursii</i> Milne-Edwards and Haime, 1848	W Antarctic Peninsula	500	Gonochoric	4800 µm	2412 opp
<i>Flabellum curvatum</i> Moseley, 1881	W Antarctic Peninsula	500	Gonochoric	5120 µm	1618 opp
<i>Flabellum impensum</i> Squires, 1962	W Antarctic Peninsula	500	Gonochoric	5167 µm	1270 opp

Key – (I) Inferred: opp = oocytes per polyp; ocm<sup>2</sup> = oocytes per cm<sup>2</sup> of skeletal material  
References: 1 Waller et al. 2002; 2 Flint 2003; 3 Waller and Tyler in press; 4 Brooke pers com; 5 Waller et al. in press; 6 Brooke and Young 2003; 7 Waller 2003; 8 Burgess and Babcock 2005

**Table 1** continued

Method	Production	Release	Larvae	Notes	Ref
Spawner	Continuous		(I) Lecithotrophic		1
Spawner	Continuous		(I) Lecithotrophic		2
(I) Spawner	June/Aug	Jan/Feb	(I) Lecithotrophic		3
				Nov. only	4
Spawner	Periodic		(I) Lecithotrophic	Female Only	3
				Male Only	8
Spawner	Continuous		(I) Lecithotrophic		5
Spawner	Continuous (sequential)		(I) Lecithotrophic		5
Spawner	Continuous (sequential)		Planktotrophic		5
Spawner	early summer	late summer/fall	Lecithotrophic?		6
Spawner	Continuous		(I) Lecithotrophic		7
Spawner	Continuous		(I) Lecithotrophic		7
Spawner	Continuous		(I) Lecithotrophic	One sample	8
Spawner	Seasonal			One sample	8
Spawner	Seasonal			One sample	8
Broods	Seasonal?		Brooded		7
Broods	Continuous?		Brooded		7
Broods	?		Brooded		7

## Gamete release

There are just three records of brooding in deep-water scleractinians from the Antarctic deep continental shelf. Waller (2003) observed brooded planulae in the mesenteries of *Flabellum impensum*, *F. curvatum* and *F. thouarsii*. All other species reported, both reef building and solitary, appear to spawn their gametes into the water column for external fertilisation (Table 1). Waller (2003) however suggests that these three Antarctic species, though found at 500 m, follow reproductive patterns more common amongst shallow Antarctic fauna than deep-water. Broadcast spawning is also more prevalent than brooding in shallow-water species of scleractinian (Richmond and Hunter 1990). Indeed, Stimson (1978) suggested deeper-living corals should spawn gametes rather than brood, to aid wide dispersal needed to find suitable substratum.

Gametogenesis can either be quasi-continuous (Waller et al. 2002; Flint 2003; Burgess and Babcock 2005; Waller et al. in press), periodic (Waller and Tyler in press) or seasonally-controlled (Brooke 2003; Waller and Tyler in press). The majority of shallow-water scleractinians have some form of seasonality, usually controlled by temperature or lunar periodicity (Fadlallah 1983; Harrison and Wallace 1990; Richmond and Hunter 1990). Seasonality in the deep-sea environment has been debated for a number of years (see Gage and Tyler 1991). In most areas, these deep-sea species live below the permanent thermocline, so there is little seasonal fluctuation in temperature. However, there is a seasonal fluctuation in phytodetritus to depth that has been associated with seasonal reproduction in several species of echinoderms and bivalves (Billett et al. 1983; Tyler et al. 1992, 1993; Rice and Lamshead 1994). Waller and Tyler (in press) also suggest the seasonal reproduction found in *Lophelia pertusa*, and the periodic reproduction found in *Madrepora oculata* from the NE Atlantic may also be related to the phytodetrital fall.

## Larval development

There have been numerous studies concerning the larval biology and development of shallow-water scleractinians (Rinkevich and Loya 1979; Szmant-Froelich et al. 1980; Fadlallah and Pearse 1982; Tranter et al. 1982). These corals have proved to be ideal candidates for larval ecology, spawning freely when cued by either heat shock (Szmant-Froelich 1980; Fadlallah 1983) or the addition of gametes from the opposing sex (Szmant-Froelich 1980; Tranter et al. 1982).

Deep-water scleractinians, as yet, have proved more difficult to spawn. Trials of heat and cold shock were applied to numerous colonies of *Lophelia pertusa* and *Madrepora oculata* during three cruises in the NE Atlantic (RRS *Discovery* cruises 248, 260 and 266) with no success (Waller 2003).

Brooke (2002) had more success with *Oculina varicosa*, with deep-water colonies observed broadcast spawning after collection. Brooke and Young (2003) is the only detailed study to date on the larval ecology of a deep-water scleractinian. *O. varicosa* produced ciliated planula larvae and patterns of embryogenesis were observed to be similar to those of shallow-water species. These planulae were small

(~100  $\mu\text{m}$ ) when compared to the maximum oocyte sizes of other species studied (Table 1), and thus likely to be planktotrophic (Brooke and Young 2003).

## Settlement

Brooke (2002) found deep-water *O. varicosa* larvae to remain active for over a month, but the larvae also probed the bottom after 10-14 days, suggesting they are ready to metamorphose. The wide dispersal of many species of deep-water scleractinian would suggest the competency periods of larvae to be long (Rogers 1999), but there are as yet no data to support this.

Brooded planulae tend to have shorter competency times, settling immediately after one or two days (Fadlallah and Pearse 1982; Szmant-Froelich et al. 1985). Broadcasting species tend to settle after 4-6 days (Schlesinger and Loya 1985; Babcock and Heyward 1986; Sakai 1997). Some brooded planulae have a longer larval life. Richmond (1997) estimated larval competency to be over 100 days in *Pocillopora damicornis*. It is possible that this extended period is likely to be due to the zooxanthellae found in these brooded planulae providing extra energy reserves (Richmond 1997). Deep-water species are, however without zooxanthellae, therefore the larval planktonic phase may be shorter, though there is as yet no data.

It is thought that the larvae of deep-water scleractinians require a hard substratum, such as a rock outcrop, or shell or worm tube in sandy areas, for settlement to occur (Wilson 1979; Rogers 1999). Many colonies of *Lophelia pertusa*, *Desmophyllum cristagalli*, *Enallopsammia rostrata* have been observed attached to rocky outcrops or dead gorgonian and scleractinian skeletons in the northern Atlantic (Adkins and Schierer 2003).

## Discussion

In shallow waters the pattern of reproduction is highly variable both between and within species (Fadlallah 1983; Richmond and Hunter 1990). These interspecific differences are thought to be due to environmental adaptations, and so are also likely to occur within deep-water species. Within the genus *Caryophyllia*, *C. clavus* and *C. smithii* are gonochoric species (Tranter et al. 1982; Fadlallah 1983), however three species of deep water *Caryophyllia* have all been shown to be hermaphroditic (Waller et al. in press). Of the five species of *Flabellum* studied, three brood their young, and two broadcast (Waller 2003).

In the western Atlantic, Brooke (2002) found shallow-water colonies of *O. varicosa* to have the same seasonal pattern of reproduction as the deeper-living colonies suggesting little environmental control in this case. Flint (2003) observed *Fungiacyathus marenzelleri* from 4000 m in the NE Pacific to have similar seasonal cycle as that described by Waller et al. (2002) at 2000 m in the NE Atlantic. However, fecundity was significantly different, with the deeper individuals producing fewer oocytes, possibly a result of reduced food availability at these greater depths.

While there is evidence for both phylogenetically and environmentally constrained reproduction, reproductive studies in definitive areas are required to

allow an adequate assessment of conservation potential. Understanding reproductive processes of a species in a single area, though providing a baseline, cannot be guaranteed to be the pattern observed in other areas.

The main aim of this review is to demonstrate the paucity of biological information that is available on deep-sea corals. Reproduction is one of the most fundamental biological processes and an understanding of it must be attained to complete any conservation or management effort. The intense trawling damage now observed globally (Probert et al. 1997; Koslow and Gowlett-Jones 1998; Bett 2001; Brooke 2002; Hall-Spencer et al. 2003; Wheeler et al. in press) has highlighted the need to attain ecological and biological data quickly, before these areas are damaged beyond repair. Without this information we would have no insight as to this habitats ability, and speed, of re-colonisation after a damaging event.

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