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SHORT COMMUNICATION

It pays to have a big mouth: mushroom corals ingesting salps at northwest Borneo

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Abstract During daytime dives in July 2011 on the reefs of Kota Kinabalu (Sabah, Malaysia), large quantities of slow-moving salps (Tunicata: Thaliacea: Salpida) were observed. Some of these were seen to be caught and ingested by various mushroom corals (Fungiidae) and an anchor coral (Euphylliidae). The predators had complete salps (2–6 cm long) or partly digested salp remnants stuck inside their wide-open mouths. Salps that were observed landing on top of mushroom corals did not escape. They became captured by tentacles and were transported towards the opening coral mouths. To our knowledge, the present in situ observation is the first record of numerous salps being consumed by corals. All the observed predating coral species, either belonging to monostomatous or polystomatous species, possessed large mouths. The presence of multiple mouths enables mushroom corals to become larger than those with single mouths. Because a large polyp size facilitates the capture of food, it is advantageous for them to be polystomatous, especially when they possess a large mouth.

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Introduction

In recent decades much attention has been given to the symbiotic relationship between reef corals and their symbiotic algae (zooxanthellae), which became particularly apparent with the occurrence of coral bleaching (e.g. Hoeksema 1991a; Brown 1997; Sampayo et al. 2008; Suggett and Smith 2011; Hoeksema and Matthews 2011). Because of the increasing emphasis on reef corals as autotrophs, it almost seemed that their other role as heterotrophs (Goreau et al. 1971; Porter 1974, 1976; Bak et al. 1998; Houlbrèque and Ferrier-Pagès 2009; Tremblay et al. 2011) became less noticed.

Many observations regarding food intake by reef corals resulted from experiments that focused on their feeding mechanism (Boschma 1925; Sorokin 1981; Clayton and Lasker 1982; Sebens and Johnson 1991; Sebens et al. 1996, 1998; Coles 1997; Ferrier-Pages et al. 2003). In comparison, only a few studies focused on their specific prey, which predominantly consists of small demersal and planktonic animals like amphipods, copepods, nematodes, nemerteans, nereids, polychaetes, and jellyfish, as found in their gut contents (Boschma 1924; Porter 1974; Lewis and Price 1975; Johnson and Sebens 1993). Furthermore, it is assumed that prey is predominantly caught by corals that are active at night (Houlbrèque and Ferrier-Pagès 2009).

Monostomatous mushroom corals (Scleractinia: Fungiidae) are iconic for having large polyps with a single, large mouth. They have been used in various classic studies on feeding mechanisms (Duerden 1906; Boschma 1924, 1926; Yonge 1930; Abe 1938; Stephens 1962; Schuhmacher 1979). Polystomatous species are usually larger owing to their additional (secondary) mouths, which are either smaller or equal in size compared to the primary mouth (Hoeksema 1991b; Gittenberger et al. 2011).

During a recent biodiversity survey on the coral reefs of Kota Kinabalu, we observed several monostomatous and polystomatous mushroom corals preying on salps (Thaliacea: Salpida: Salpidae). To our knowledge, the feeding of corals on salps has been reported only once before, which was based on a single salp found in the gut contents of a colony of *Montastraea cavernosa* (Linnaeus, 1776) (see Porter 1974).

Materials and methods

A faunistic study of mushroom corals was performed in the period 16–28 July 2011 on the coral reefs of Kota Kinabalu, the capital of Sabah, Malaysia (5° 57'–6° 5'N, 115° 59'–116° 5'E). Thirty dives, each approximately 1 h in duration, were made using SCUBA. The roving diver technique was employed (see e.g., Hoeksema and Koh 2009), in which species incidence data were recorded at each reef over the whole depth range where corals occurred, from the reef flat to the reef base, but not deeper than 30 m. At 3–18 m depth, several mushroom corals had their mouths wide open. Closer examination revealed that these corals had caught transparent salps. We also encountered slow-swimming salps in the water column. An inventory was made of which recorded mushroom coral species appeared to prey on salps. An additional remark is given on a non-mushroom coral with a salp in its mouth.

Results

All but one of the observed salp-predating corals belong to the mushroom coral family Fungiidae (Hoeksema 1989; Gittenberger et al. 2011). Nine of the 34 recorded mushroom coral species were observed to prey on salps (Table 1). Specimens of *Cycloseris costulata*, *C. fragilis*, *Danafungia scruposa*, *Fungia fungites*, *Pleuractis moluccensis*, and *P. paumotensis* had transparent salps (ca. 2 cm) or their remnants stuck inside their wide-open mouths (Fig. 1a, d–g). An individual of *Heliofungia actiniformis* had a salp of ca. 6 cm captured by its long tentacles (Fig. 1h). Two salps that had landed on top of *D. scruposa* corals were transported by tentacles from the coral margin towards the opening mouth, which was slightly hindered by some wave action. The salps hardly moved by themselves and did not attempt to escape. Polystomatous corals of *Halomitra pileus* and *Herpolitha limax* had salps only in their largest mouths (Fig 1b, c). Apart from mushroom corals, the only other salp-consuming coral observed was a

Table 1 Records of mushroom coral species (n=34) and those predating on salps present on Kota Kinabalu reefs indicated by number of sites (total 30)

Species	Number of sites	With salp predation
Ctenactis albitentaculata Hoeksema 1989	10	-
Ctenactis echinata (Pallas, 1766)	28	-
Ctenactis crassa (Dana, 1846)	29	-
Cycloseris costulata (Ortmann, 1889)	28	2
Cycloseris cyclolites (Lamarck, 1815)	9	-
Cycloseris fragilis (Alcock, 1893)	21	1
Cycloseris mokai (Hoeksema 1989)	27	-
Cycloseris sinensis Milne Edwards & Haime, 1851	15	-
Cycloseris somervillei (Gardiner, 1909)	2	-
Cycloseris tenuis (Dana, 1846)	15	-
Danafungia horrida (Dana, 1846)	29	-
Danafungia scruposa (Klunzinger, 1879)	29	3
Fungia fungites (Linnaeus, 1758)	30	3
Halomitra pileus (Linnaeus, 1758)	12	1
Heliofungia actiniformis (Quoy & Gaimard, 1833)	28	1
Herpolitha limax (Esper, 1797)	30	3
Lithophyllon concinna (Verrill, 1864)	30	-
Lithophyllon repanda (Dana, 1846)	30	-
Lithophyllon scabra (Döderlein, 1901)	19	-
Lithophyllon spinifer (Claereboudt & Hoeksema, 1987)	7	-
Lithophyllon undulatum Rehberg, 1893	26	-
Lobactis scutaria (Lamarck, 1801)	19	-
Pleuractis granulosa (Klunzinger, 1879)	29	-
Pleuractis gravis (Nemenzo, 1955)	21	-
Pleuractis moluccensis (Van der Horst, 1919)	30	4
Pleuractis paumotensis (Stutchbury, 1833)	30	1
Pleuractis taiwanensis (Hoeksema and Dai, 1901)	2	-
Podabacia crustacea (Pallas, 1766)	23	-
Podabacia motuporensis Veron, 1990	1	-
Podabacia sinai Veron, 2000	4	-
Polyphyllia talpina (Lamarck, 1801)	28	-
Sandalolitha dentata Quelch, 1884	20	-
Sandalolitha robusta (Quelch, 1886)	29	-
Zoopilus echinatus Dana, 1846	1	-

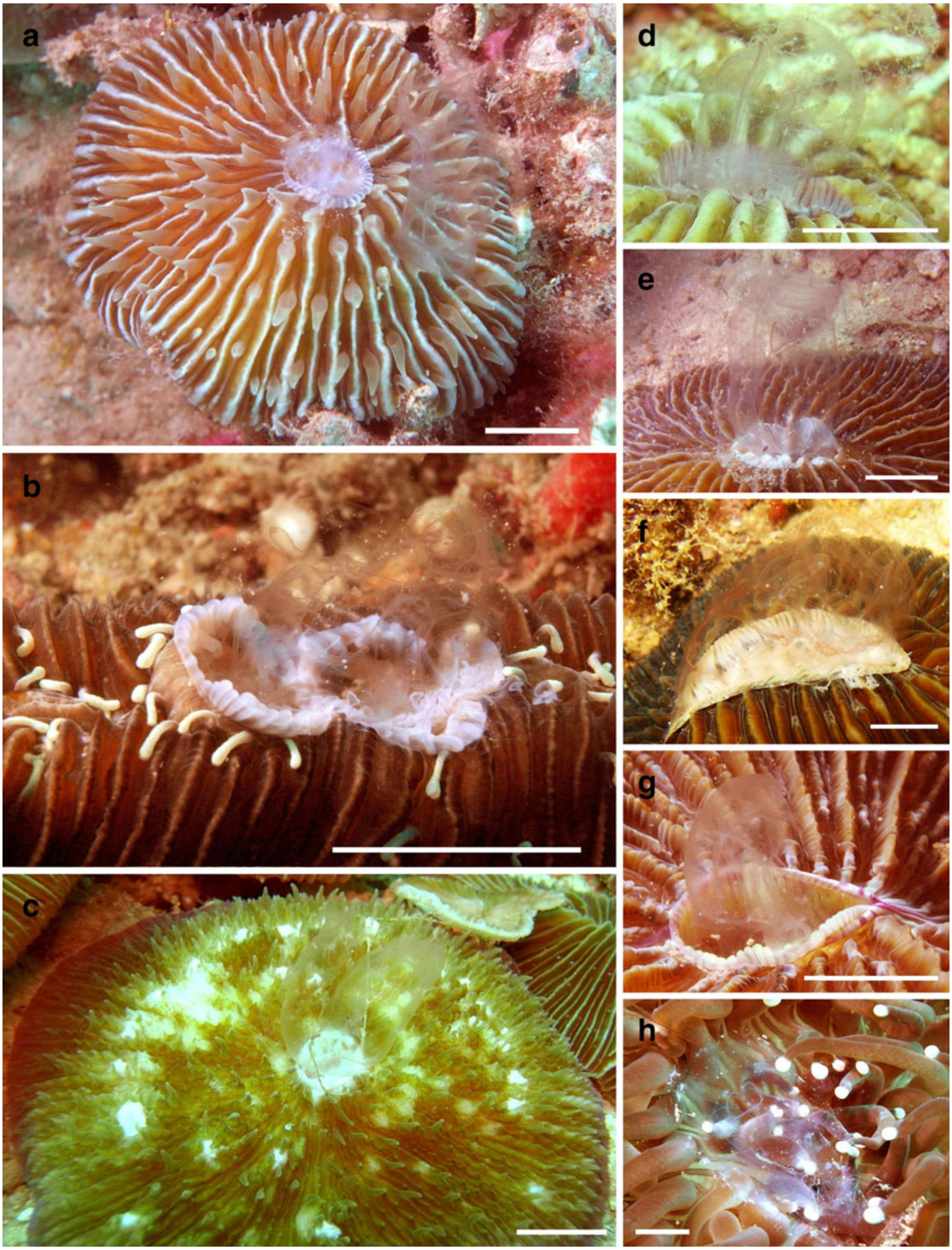

Fig. 1 Mushroom corals of various species feeding on transparent salps at Kota Kinabalu, Sabah: **a** *Danafungia scruposa* (one salp in mouth and one beside), **b** *Herpolitha limax* (two mouths sharing one salp), **c** *Halomitra pileus*, **d** *Cycloseris costulata*, **e** *Pleuractis paumotensis*, **f** *P. moluccensis*, **g** *Fungia fungites*, **h** *Heliofungia actiniformis*. *Scale bars* 1 cm

specimen of *Euphyllia paraancora* Veron, 1990 (Fig. 2). Some mushroom corals appeared to ingest their prey by showing barely visible salp remnants inside their wide-open mouth (Fig. 3).

The salps most probably belong to the subfamily Salpinae (R.W.M. Van Soest, personal communication); for salp taxonomy and phylogeny, see Godeaux (1998), Van Soest (1998) and Govindarajan et al. (2011).

Fig. 2 Specimen of *Euphyllia paraancora* with a captured salp at Kota Kinabalu, Sabah. *Scale bar* 1 cm

Discussion

Although it is known that many species of corals can be active heterotrophs, ingesting organisms ranging from bacteria to mesozooplankton, there is very little information on what animals are eaten by corals (Houlbrèque and Ferrier-Pagès 2009). It was recently discovered that individuals of the monostomatous fungiid *Danafungia scruposa* are able to prey on large jellyfish (diameter up to 12 cm) in the Red Sea (Alamaru et al. 2009). In an earlier anecdotal account based on an aquarium experiment, it was reported that the mushroom coral *Heliofungia actiniformis* is able to use its long tentacles to predate on 1.5 cm long damselfish (Sisson 1973). Because little is known about the diet of corals and other anthozoans (see e.g., Van der Meij and Reijnen 2011), it is important that field observations concerning this topic are reported.

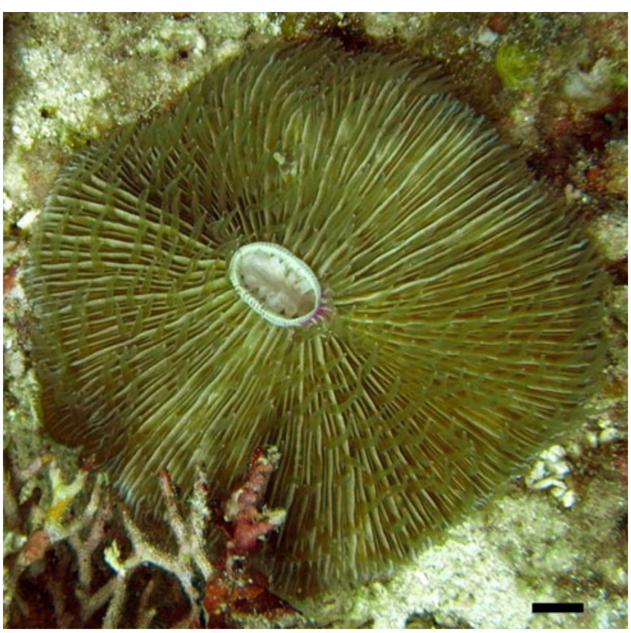

Fig. 3 Specimen of *Fungia fungites* with a partly ingested salp at Kota Kinabalu, Sabah. *Scale bar* 1 cm

It is also relevant to note that some commensal animals are able to live in between the tentacles of mushroom corals without being eaten, such as particular species of fish and shrimp (Bos 2011; Hoeksema and Fransen 2011; Hoeksema et al. 2011). It is unclear whether they are immune to the coral venom and therefore escape predation.

Until recently, gelatinous zooplankton, like salps, ctenophores and pelagic cnidarians, were considered ‘trophic dead ends’ in food webs, i.e. zooplanktivores that seemed to lack obvious top predators themselves (Mianzan et al. 2001). However, various animals are known to eat salps, such as sea lions (Childerhouse et al. 2001), albatrosses (James and Stahl 2000), turtles (Van Nierop and Den Hartog 1984; Hatase et al. 2002; Eckert 2006; Dodge et al. 2011), fish (Lyle and Smith 1997; Morato et al. 2000; Mianzan et al 2001), and krill (Kawaguchi and Takahashi 1996).

To our knowledge, the present report is the first record dealing with corals in the process of capturing and eating salps, although Caribbean corals of *Agaricia agaricites* (Linnaeus, 1758) have also been observed to ingest planktonic tunicates (R.P.M. Bak, personal communication). With regard to the different growth forms of mushroom corals, the present observations suggest that a large surface area may facilitate catching food, while big mouths enable feeding on large prey when available. Both traits are extra advantageous when combined, like in most polystomatous fungiids (Hoeksema 1991b; Gittenberger et al. 2011). In cases where mushroom corals form dense aggregations (e.g. Hoeksema 2004; Hoeksema and Matthews 2011), salps may not easily escape capture. However, if the aggregations consist of regenerated mushroom coral fragments (Hoeksema and Gittenberger 2010; Hoeksema and Waheed 2011), only a few of them possess large primary mouths that may be used to ingest large prey.

Although it is advantageous for corals to have a large mouth if large prey is available, it is not clear whether they are as efficient when small prey is more abundant than large prey. In this instance, many small mouths might be more ideal because a particular polyp (or mouth) size may indicate a specific size spectrum of prey (Tsounis et al. 2010). This is beneficial for various mushroom coral species that have secondary small mouths in addition to a large primary mouth (Hoeksema 1991b; Gittenberger et al. 2011). Prey behaviour and environmental factors may interfere with the capture success of corals regardless of their polyp size (Sebens et al. 1996; Palardy et al. 2005). The prey intake by some mushroom corals was only slightly delayed by minor wave action. Stronger water movement at shallow depths may increase the probability of transporting the large salps away from their predators.

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References

Abe N (1938) Feeding behaviour and the nematocyst of *Fungia* and 15 other species of corals. Palao Trop Biol Sta Stud 3: 469–521

Alamaru A, Bronstein O, Loya Y, Dishon G (2009) Opportunistic feeding by the fungiid coral *Fungia scruposa* on the moon jellyfish *Aurelia aurita*. Coral Reefs 28:865

Bak RPM, Joenje M, De Jong I, Lambrechts DYM, Nieuwland G (1998) Bacterial suspension feeding by coral reef benthic organisms. Mar Ecol Prog Ser 175:285–288

Bos AR (2011) Symbiotic fishes (Gobiidae and Labridae) of the mushroom coral *Heliofungia actiniformis* (Scleractinia; Fungiidae). Coral Reefs. doi:10.1007/s00338-011-0834-3

Boschma H (1924) On the food of Madreporaria. Proc K Akad Wet Amst 27:13–23

Boschma H (1925) On the feeding reactions and digestion in the coral polyp *Astrangia danae*, with notes on its symbiosis with zooxanthellae. Biol Bull 49:407–439

Boschma H (1926) On the food of reef-corals. Proc K Akad Wet Amst 29:993–997

Brown BE (1997) Coral bleaching: causes and consequences. Coral Reefs 16(Suppl):S129–S138

Childerhouse S, Dix B, Gales N (2001) Diet of New Zealand sea lions (*Phocarctos hookeri*) at the Auckland Islands. Wildl Res 28:291–298

Clayton WS, Lasker HR (1982) Effects of light and dark treatments on feeding by the reef coral *Pocillopora damicornis* (Linnaeus). J Exp Mar Biol Ecol 63:269–279

Coles SL (1997) Quantitative estimates of feeding and respiration for three scleractinian corals. Limnol Oceanogr 14:949–953

Dodge KL, Logan JM, Lutcavage ME (2011) Foraging ecology of leatherback sea turtles in the Western North Atlantic determined through multi-tissue stable isotope analyses. Mar Biol 158:2813–2824

Duerden JE (1906) The role of mucus in corals. Q J Microsc Sci 49:591–614

Eckert SA (2006) High-use oceanic areas for Atlantic leatherback sea turtles (*Dermochelys coriacea*) as identified using satellite telemetered location and dive information. Mar Biol 49:1257–1267

Ferrier-Pages C, Witting J, Tambutte E, Sebens KP (2003) Effect of natural zooplankton feeding on the tissue and skeletal growth of the scleractinian coral *Stylophora pistillata*. Coral Reefs 22:229–240

Gittenberger A, Reijnen BT, Hoeksema BW (2011) A molecularly based phylogeny reconstruction of mushroom corals (Scleractinia: Fungiidae) with taxonomic consequences and evolutionary implications for growth forms and life history traits. Contrib Zool 80:107–132

Godeaux J (1998) The relationships and systematic of the Thaliacea, with keys for identification. In: Bone Q (ed) The biology of pelagic tunicates. Oxford University Press, Oxford, pp 273–294

Goreau TF, Goreau NI, Yonge CM (1971) Reef corals: autotrophs or heterotrophs? Biol Bull 141:247–260

Govindarajan AF, Bucklin A, Madin LP (2011) A molecular phylogeny of the Thaliacea. J Plankton Res 33:843–853

Hatase H, Takai N, Matsuzawa Y, Sakamoto W, Omuta K, Goto K, Arai N, Fujiwara T (2002) Size-related differences in feeding habitat use of adult female loggerhead turtles *Caretta caretta* around Japan determined by stable isotope analyses and satellite telemetry. Mar Ecol Prog Ser 233:273–281

Hoeksema BW (1989) Taxonomy, phylogeny and biogeography of mushroom corals (Scleractinia: Fungiidae). Zool Verh 254:1–295

Hoeksema BW (1991a) Control of bleaching in mushroom coral populations (Scleractinia: Fungiidae) in the Java Sea: stress tolerance and interference by life history strategy. Mar Ecol Prog Ser 74:225–237

Hoeksema BW (1991b) Evolution of body size in mushroom corals (Scleractinia: Fungiidae) and its ecomorphological consequences. Neth J Zool 41:122–139

Hoeksema BW (2004) Impact of budding on free-living corals at East Kalimantan. Indonesia Coral Reefs 23:492

Hoeksema BW, Fransen CHJM (2011) Space partitioning by symbiotic shrimp species cohabitating in the mushroom coral *Heliofungia actiniformis* at Semporna, eastern Sabah. Coral Reefs 30:519

Hoeksema BW, Gittenberger A (2010) High densities of mushroom coral fragments at West Halmahera. Indonesia Coral Reefs 29:691

Hoeksema BW, Koh EGL (2009) Depauperation of the mushroom coral fauna (Fungiidae) of Singapore (1860 s–2006) in changing reef conditions. Raffles Bull Zool Suppl 22:91–101

Hoeksema BW, Matthews JL (2011) Contrasting bleaching patterns in mushroom coral assemblages at Koh Tao. Gulf of Thailand. Coral Reefs 30:95

Hoeksema BW, Waheed Z (2011) Initial phase of autotomy in fragmenting *Cycloseris* corals at Semporna, eastern Sabah, Malaysia. Coral Reefs 30:1087

Hoeksema BW, van der Meij SET, Fransen CHJM (2011) The mushroom coral as a habitat. J Mar Biol Assoc UK. doi:10.1017/S0025315411001445

Houlbrèque F, Ferrier-Pagès C (2009) Heterotrophy in tropical scleractinian corals. Biol Rev 84:1–17

James GD, Stahl JC (2000) Diet of southern Buller's albatross (*Diomedea bulleri bulleri*) and the importance of fishery discards during chick rearing. N Z J Mar Freshw Res 34:435–454

Johnson AS, Sebens KP (1993) Consequences of a flattened morphology: effects of flow on feeding rates of the scleractinian coral *Meandrina meandrites*. Mar Ecol Prog Ser 99:99–114

Kawaguchi S, Takahashi Y (1996) Antarctic krill (*Euphausia superba* Dana) eat salps. Polar Biol 16:479–481

Lewis JB, Price WS (1975) Feeding mechanisms and feeding strategies of Atlantic reef corals. J Zool 176:527–544

Lyle JM, Smith DC (1997) Abundance and biology of warty oreo (*Allocyttus verrucosus*) and spiky oreo (*Neocyttus rhomboidalis*) (Oreosomatidae) off south-eastern Australia. Mar Freshwat Res 48:91–102

Mianzan H, Pájaro M, Alvarez Colombo G, Madirolas A (2001) Feeding on survival-food: gelatinous plankton as a source of food for anchovies. Hydrobiologia 451:45–53

Morato T, Santos RS, Andrade JP (2000) Feeding habits, seasonal and ontogenetic diet shift of blacktail comber, *Serranus atricauda* (Pisces: Serranidae), from the Azores, north-eastern Atlantic. Fish Res 49:51–59

Palardy JE, Grottoli AG, Matthews KA (2005) Effects of upwelling, depth, morphology and polyp size on feeding in three species of Panamanian corals. Mar Ecol Prog Ser 300:79–89

Porter JW (1974) Zooplankton feeding by the Caribbean reef-building coral *Montastrea cavernosa*. Proc 2nd Int. Symp Coral Reefs 1:111–125

Porter JW (1976) Autotrophy, heterotrophy and resource partitioning in Caribbean reef-building corals. Am Nat 110:731–742

Sampayo EM, Ridgway T, Bongaerts P, Hoegh-Guldberg O (2008) Bleaching susceptibility and mortality of corals are determined by fine-scale differences in symbiont type. Proc Natl Acad Sci USA 105:10444–10449

Schuhmacher H (1979) Experimentele Untersuchungen zur Anpassung von Fungiiden (Scleractinia, Fungiidae) an unterschiedliche Sedimentations- und Bodenverhältnisse. Int Rev Gesamten Hydrobiol 64:207–243

Sebens KP, Johnson AS (1991) Effects of water movement on prey capture and distribution of reef corals. Hydrobiologia 226:91–101

Sebens KP, Vandersall KS, Savina LA, Graham KR (1996) Zooplankton capture by two scleractinian corals, *Madracis mirabilis* and *Montastrea cavernosa*, in a field enclosure. Mar Biol 127:303–318

Sebens KP, Grace SP, Helmuth B, Maney EJ, Miles JS (1998) Water flow and prey capture by three scleractinian corals, *Madracis mirabilis*, *Montastrea cavernosa* and *Porites porites*, in a field enclosure. Mar Biol 131:347–360

Sisson RF (1973) Life cycle of a coral. Natl Geogr Mag 143:780–793

Sorokin YI (1981) Aspects of the biomass, feeding, and metabolism of common corals of the Great Barrier Reef, Australia. Proc 4th Int Coral Reef Symp 2:27–31

Stephens GC (1962) Uptake of organic material by aquatic invertebrates. I. Uptake of glucose by the solitary coral *Fungia scutaria*. Biol Bull 123:648–659

Suggett DJ, Smith DJ (2011) Interpreting the sign of coral bleaching as friend vs. foe. Glob Change Biol 17:45–55

Tremblay P, Peirano A, Ferrier-Pagès C (2011) Heterotrophy in the Mediterranean symbiotic coral *Cladocora caespitosa*: comparison with two other scleractinian species. Mar Ecol Prog Ser 422:165–177

Tsounis G, Orejas C, Reynaud GJM, Allemand D, Ferrier-Pagès C (2010) Prey capture rates by four Mediterranean cold water corals. Mar Ecol Prog Ser 398:149–155

Van der Meij SET, Reijnen BT (2011) First observations of attempted nudibranch predation by sea anemones. Mar Biodivers. doi:10.1007/s12526-011-0097-9

Van Nierop MM, Den Hartog JC (1984) A study on the gut contents of live juvenile loggerhead turtles, *Caretta caretta* (Linnaeus) (Reptilia, Cheloniidae), from the south-eastern part of the North Atlantic Ocean, with emphasis on coelenterate identification. Zool Meded 59:35–54

Van Soest RWM (1998) The cladistic biogeography of salps and pyrosomas. In: Bone Q (ed) The biology of pelagic tunicates. Oxford University Press, Oxford, pp 231–249

Yonge CM (1930) Studies on the physiology of corals I. Feeding mechanism and food. Sci Rep Great Barrier Reef Exp 1(1928-29):1–57