Effect of Depth on Sponge Assemblage Structure at Palmyra Atoll, Central Pacific

Ingrid S. S. Knapp* and James J. Bell

Centre for Marine Environmental and Economic Research, School of Biological Sciences, Victoria University of Wellington, P.O. Box 600, Wellington, New Zealand

Abstract: We examined the influence of depth on sponge assemblages across three lagoons at Palmyra; a remote atoll situated in the Central Pacific. The atoll is unusual in that it was heavily altered during WWII resulting in an atypical lagoon system. We conducted surveys at both 6-8m and 12-14m at 3 sites at the atoll and recorded sponge densities, area cover and available substrate for the 29 species found at these sites. Multivariate analysis of sponge densities and area cover revealed significant variability in sponge assemblages between both site and depth. Univariate analysis also showed significant differences in area cover between depths, but not between sites. Diversity indices and the average number of species at each site showed an increase in diversity across lagoons from West to East. This study indicates that despite the small size of the atoll, depth is a factor that shapes sponge assemblages at Palmyra Atoll. The heavy alterations to the lagoon, particularly the area near the channel entrance may be influencing the sponge assemblage structure, however, other environmental variables still need to be investigated.

Keywords: Sponge, depth, Palmyra Atoll, sedimentation, Central Pacific, flow rate.

INTRODUCTION

To examine and identify the ecological processes that shape assemblages, species abundance and distribution patterns must first be described. Sponges are an important component of benthic fauna that are highly diverse as well as being an ecologically important invertebrate taxon. Despite their importance, sponges are vastly and notoriously understudied [1, 2] even though on some reefs, sponges can even exceed the species diversity and biomass of the scleractinian corals [3]. Understandably, due to the remoteness of some locations, such as Palmyra Atoll (located in the Central Pacific), accessibility for researchers can seriously limit our understanding of these assemblages. In the case of Palmyra Atoll, it is only through its recent co-ownership by The Nature Conservancy (TNC) and the U.S Fish and Wildlife Service (USFWS) in 2001, that this remote atoll can now be extensively studied. Palmyra is of particular interest to scientists because it remains one of the few 'near pristine' reef systems left in the world [4].

Palmyra consists of many islets with shallow lagoons surrounded by an extensive reef system. The lagoons were essentially an unaltered system until the Second World War when the U.S. Navy occupied the atoll making major alterations. The work included enlarging the islets, creating an entrance channel for boats, dredging the lagoons and building a central causeway to connect two islets, effectively interrupting the water flow between lagoons [5]; this would likely have had serious impacts on the marine fauna of the lagoons.

*Address correspondence to this author at the Centre for Marine Environmental and Economic Research, School of Biological Sciences, Victoria University of Wellington, P.O. Box 600, Wellington, New Zealand; Tel: 04-463-5109; E-mail: ingrid.knapp@vuw.ac.nz

Sponges form an important part of subtidal benthic communities and inhabit most marine ecosystems [6, 7]. The widespread distribution of this phylum is most likely due to a number of adaptive features including efficient suspension feeding capabilities [8, 9] and the ability to regenerate [10, 11]. Depth has long been recognised as a strong influencing factor on marine benthic community structure [12, 13] and therefore an important factor to consider when conducting surveys of new locations to understand assemblage structure.

The atoll system at Palmyra, like the rest of the Line Islands, is unusual in that large macro-invertebrates including sponges are uncommon on the outer reef systems (S. Godwin *pers. Obs*.) [4], usually an ecosystem abundant in such fauna e.g. in the Caribbean and the Indo-Pacific [3, 14, 15]. The reef system is considered 'near pristine', however, the lagoon is far from its original state. Lagoons, are generally low current systems and act like sediment 'sinks' and suffer from high levels of sedimentation [16]. Sponges, like many marine invertebrates are suspension feeders and as such obtain oxygen and food in the form of organic carbon from the water column [17]. High levels of sediment may clog the delicate filtering apparatus of sponges [18, 19]. However, they have been commonly documented inhabiting areas of high sedimentation [14, 16, 20] [21, 22] and it is therefore of considerable interest to understand the distribution patterns of sponges within the lagoon system at Palmyra Atoll, particularly as it is an altered environment.

Understanding the diversity and abundance of sponges in the lagoons at Palmyra is also very important from a management perspective because the diversity, distribution and abundance of sponge assemblages is presently unknown, despite sponges appearing to be the dominant fauna of the lagoon environment. The lagoons at Palmyra are densely populated with sponges, however, little is known of their potential impact on the surrounding ecosystem or whether

1874-4508/10

they are even native to Palmyra or were introduced during military occupation. Furthermore, another important reason to survey and study the sponges at Palmyra is that the lagoons are very shallow in places; areas of low water flow and the high sponge biomass could potentially remove large quantities of nutrients and oxygen from the water column [23, 24]. Therefore, changes in sponge assemblages have the potential to affect the environment and organisms in the lagoons and even the reef as the water flows out across the reef systems [25].

The aim of this study is to determine the effect of depth on sponge assemblages at three different sites in the lagoon system at Palmyra Atoll. We quantified the sponge species density, cover, diversity and evenness, relative to the available boulder substrate at these different sites and depths.

METHODS AND MATERIALS

Study Site

Palmyra Atoll is located at the North-western end of the Line Islands (5°53'N, 162°05'W), 1930 km south of Hawaii (Fig. **1**). The atoll was designated a National Wildlife refuge in 2001 is now jointly owned by The Nature Conservancy and U.S. National and Fish and Wildlife. Palmyra is listed as one of the U.S. Pacific Remote Island Areas (PRIAs) and in 2009 became part of the Pacific Remote Islands Marine National Monument (8336).

Sampling Design

Surveys were conducted using SCUBA within the lagoons at Palmyra Atoll (See Fig. **1**) between June to July and October to November 2008. Sponge assemblages were sampled at three sites across the three main lagoons at shallow (6-8m) and deep (12-14m) water sites. Fig. (**1**) indicates the location of the sites within the three lagoons. Site 1 is located in the Western lagoon adjacent to Strawn Island (05° 53'.318"N, 162° 05'.860"W). Site 2 is in the Central lagoon on the south west side of the North-South causeway (05° 53'.246"N, 162° 03'.880"W) and site 3 is north east of the Eastern lagoon just south of Aviation Island (see [5] for all island names); from here on each site is referred to by the name of the lagoon in which it is found, although it is not necessarily considered to represent the lagoon as a whole. The sites are characterised as having sandy slopes (40-50°) with small boulders generally < 1 m with negligible current flow rates (<0.05 cm^2sec^{-1}) and low boulder disturbance levels.

At each of the three sites, 10 x $1m^2$ quadrats (divided into 20 x 20 cm sub-sections) were haphazardly placed over clusters of boulders and surveyed by counting the number of individual sponge patches (sponge density) and estimating the percentage area covered and available substrata for each species per sub-section. Sponge density and cover values were then adjusted to the total amount of available substrate to provide sponge abundance data per m^2 of available substrate. Each species was given a number ID based on preliminary laboratory analysis (although these species have been distinguished they have not currently been identified).

Statistical Analyses

To characterise sponge assemblages, and compare them between sites and depths a number of indices were calculated including: number of species (S); Hill's numbers N1 and N2 and the modified Hill's ratio (N21') [26]. The Hill's N1 and Hill's N2 assess species diversity by examining the influence of rare and dominant species on assemblage structure, respectively. The modified Hill's ratio examines species equitability (evenness).

Spatial patterns of sponge densities and area occupied across the factors 'sites' and 'depths' were examined using a 2 factor nested permutational multivariate analysis of variance (PERMANOVA) with 9999 permutations [27] based on a zero-adjusted Bray-Curtis similarity matrix. The

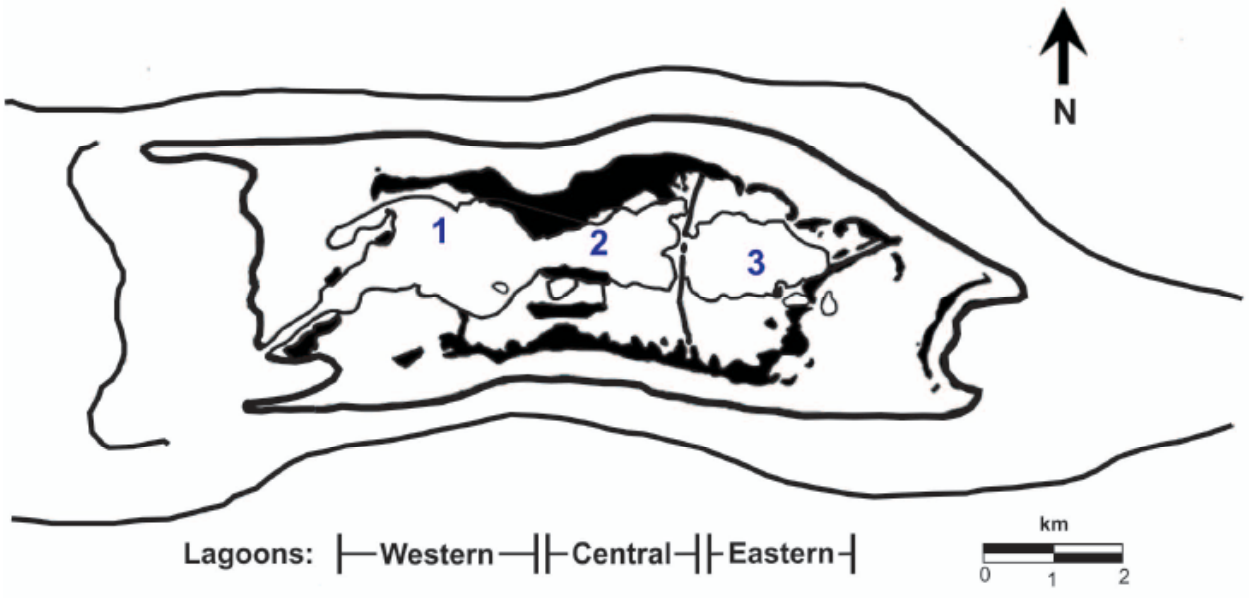

Fig. (1). Map of Palmyra with sites surveyed across the 3 lagoons at Palmyra Atoll. Site: 1= Strawn (Western lagoons), 2= South Cut (Central lagoon), 3= Aviation (Eastern lagoon).

nature of the nested design used in the PERMANOVA test means any significant difference between depths is strictly relative to the sites within which they are nested. Site was a random factor (3 levels) with depth a fixed factor (2 levels) nested within sites. Pairwise *post hoc* tests were also carried out on significant factors from the main test. Univariate analyses of sponge densities and area covered at the different sites and depths were also conducted using PERMANOVA. All data was transformed using the dispersion weighting pre-treatment, which negates the effect of spatial clustering [28], a characteristic of phyla (such as sponges) where species are known to reproduce asexually through budding, fragmentation and gemmule formation [29]. All analyses were conducted using the PRIMER v6 statistical package [26] in combination with the PERMANOVA+ add-on package [30].

RESULTS

A total of 29 distinct species were identified across all sites and depths; 15 species were found at both depths at the Western lagoon site, 19 species were found at Eastern lagoon site at both depths, while 15 species were found at the shallow site and 19 at the deep site at the Central lagoon site. Despite the similarity in the total number of species between sites and depths, assemblage composition differed considerably. The mean sponge densities (± SE) are shown in Fig. (**2**) and range from 37 (±5.9) (Western-deep) to 72 (±13.7) (Eastern-shallow) sponges m^{-2}, with a mean of 51 (±9.6) sponges m^{-2}across all three sites. The mean average sponge percentage cover across all sites was 15.2% (±2.8) with a range of 10.6% (±1.8) (Western-deep) to 20.8% (±1.9) (Western-shallow). Analysing sponge densities with a PERMANOVA test showed no significant differences between sites or depths (pseudo-F= 2.19; p= 0.07, pseudo-F= 2.09; p= 0.06 respectively). Sponge percentage cover also showed no significant difference between sites (pseudo-F= 1.31, p=0.26), but there was a significant difference between depths ($p<0.05$).

Fig. (**2**) shows that the Western lagoon site had the lowest mean number of species (S=7-8), and the Eastern lagoon site had the highest number of species (S=9-12), while the central lagoon had S=8-10. The Hill indices N1, N2 and the modified ratio N21' in Fig. (**2**) indicate similar diversity patterns amongst sites and depths. The Western lagoon site (shallow and deep water sampling locations) had the lowest diversity and the Eastern lagoon site (shallow and deep sampling locations) the highest.

Sponge assemblages were significantly different between the 2 factors, 'site' and 'depth' when analysing both sponge counts and area cover (PERMANOVA, $p<0.001$). Furthermore, PERMANOVA pairwise comparisons also found significant ($p<0.001$) differences between all sites and depths.

DISCUSSION AND CONCLUSION

The total number of species was similar at all sites, but sponge assemblages were significantly different between all sites and all depths (with depths nested within sites) across the lagoon system at Palmyra Atoll. We found no significant difference for univariate analyses of sponge densities, but we did find a significant difference between depth and area occupied. The average number of species along with the species diversity indices; N1, N2 and the modified ratio N21', indicate an increase in species numbers and diversity from the Western to Eastern lagoon sites.

Sponge assemblages vary considerably across environmental gradients [21, 31-33], therefore it is unsurprising that this study has shown differences in assemblage structure and area occupied with changes in depth even on a local-scale across lagoons in an atoll 6 km long. Previous studies have shown that sponge species distribution and abundance often vary on small spatial scales [6, 29, 31]. The explanation for the variability in assemblage structure with depth in our study is, however, unlikely to be a simply result of depth, but

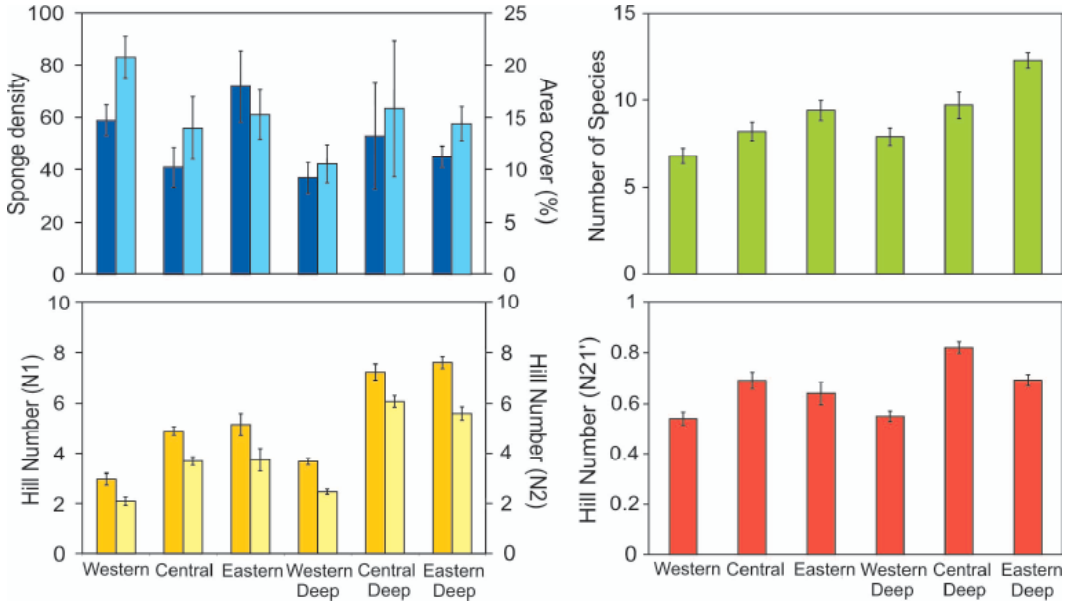

Fig. (2). Measures of sponge diversity (mean± SE) at the three sites and two depths in the lagoons at Palmyra Atoll. Shallow sites are between 6-8m and deep sites are between 12-14m. N=10 for each site. Sponge densities and percentage area occupied are adjusted to available boulder substrate.

the result of a combination of environmental factors which co-vary with depth [32]. Site-specific ecological processes that may account for the sponge assemblage structure identified in our study include; light attenuation [22], water flow regime [6], temperature [34] and oxygen concentrations [35].

Species diversity indices and species number averages indicate an increase in diversity (low to high) across the atoll from West to East. Historically, and more recently, the Western lagoon was the location of the highest levels of anthropogenic disturbance particularly during WWII [5]. The work included extensive dredging, increasing the land mass of the islets and excavating the channel through which large vessels could enter the lagoon and make safe passage to the nearby wharf (just 100m from the Western lagoon site). Habitats subject to dredging are heavily altered, removing complexity and available substrate [36, 37]. Impacts on the macrobenthos is also well documented [38, 39]. Dredging causes changes in species composition, diversity, richness [39-41] and potential permanent faunal changes [40], sometimes even resulting in complete phase shifts [42]. We suggest that the relatively higher level of disturbance at the Western lagoon has potentially lead to a site, with reduced available substrate and created conditions which is habitable by fewer species, since it has the lowest diversity, density and average number of species. The Western lagoon site, however, has the highest sponge area cover (per m^2 available substrate), which suggests that those species able to deal with the conditions in this environment have proliferated. Environmental factors, as mentioned above, may also provide a further insight into the diversity distribution of sponges across the lagoons and will be investigated in the future.

Diving restrictions at Palmyra (given it is a very remote site) limit deeper surveys, however, we have found that where there is available substrate in the lagoon at shallow depths there are abundant sponge assemblages. Therefore, we have no reason to believe this is not the case in deep waters, however, the deepest parts of the lagoons extend down to 50m and are therefore unlikely to support sponges as the waters here become anoxic (pers. comm. John Collen & Jonathan Gardner). This raises an interesting question as to the impact these abundant sponge assemblages may be having directly, as competitors, or indirectly through their efficient water filtration capabilities on other organisms. The ability of sponges to filter large quantities of water [9] has the potential to affect oxygen and nutrient levels in the lagoon, potentially influencing water quality as it leaves the lagoon and flows on to the surrounding reef. Future work will focus on broader-scale surveys of the sponge assemblages in the lagoons at Palmyra, the influence of environmental variables on distribution and the presence of sponges before the alterations.

ACKNOWLEDGEMENTS

This work could not have been possible without the help and support from Gareth Williams for diving support and data collection and Scott Godwin, Jonathan Gardner and John Collen for advisory help. We are also grateful to the staff from The Nature Conservancy (TNC), United States Fish and Wildlife service (USFWS) and the institutes involved in the Palmyra Atoll Research Consortium (PARC) for providing access to the refuge and logistical support. We are grateful to Air New Zealand, the Centre for Marine Environmental and Economic Research (CMEER), the Centre for Biodiversity and Restoration Ecology (CBRE), and Victoria University of Wellington for providing funding. This work was conducted under the special use permit #12533-08004 approved by USFWS.

REFERENCES

[1] Becerro MA. Quantitative trends in sponge ecology research. Mar Ecol 2008; 29(2): 167-77.

[2] Hooper JNA, van Soest RWM. Systema Porifera: a guide to the classification of sponges. London: Kulwer Academic/ Plenum Publishers 2002.

[3] Wulff JL. Assessing and monitoring coral reef sponges: why and how? Bull Mar Sci 2001; 69: 831-46.

[4] Sandin SA, Smith JE, DeMartini EE, *et al.* Baselines and degradation of coral reefs in the northern Line Islands. PLoS ONE 2008; 3(2): e1548.

[5] Collen J, Garton DW, Gardner JP. Shoreline changes and sediment redistribution at Palmyra Atoll (Equatorial Pacific Ocean): 1874-Present. J Coast Res 2009; 25(3): 711-22.

[6] Bell JJ, Barnes DKA. A sponge diversity centre within a marine 'island'. Hydrobiologia 2000; 440: 55-64.

[7] Witte U. Seasonal reproduction in deep-sea sponges - triggered by vertical particle flux? Mar Biol 1996; 124: 571-81.

[8] Frost IM. *In situ* measurements of clearance rates for the freshwater sponge *Spongilla lacustris*. Limnol Oceanogr 1978; 23(5): 1034-9.

[9] Vogel S. Current-induced flow through living sponges in nature. Proc Natl Acad Sci USA 1977; 74: 2069-71.

[10] Ayling AL. Growth and regeneration rates in thinly encrusting Demospongiae from temperate waters. Biol Bull 1983; 165: 343-52.

[11] Bell JJ. Regeneration rates of a temperate demosponge: the importance of water flow rate. J Mar Biol Assoc UK 2002; 82(1): 169-70.

[12] Bergen M, Weisberg SB, Smith RW, *et al.* Relationship between depth, sediment, latitude, and the structure of benthic infaunal assemblages on the mainland shelf of southern California. Mar Biol 2001; 138(3): 637-47.

[13] Underwood AJ, Kingsford MJ, Andrew NL. Patterns in shallow subtidal marine assemblages along the coast of New South Wales. Austral Ecol 1991; 16(2): 231-49.

[14] Bell JJ, Smith D. Ecology of sponge assemblages (Porifera) in the Wakatobi region, south-east Sulawesi, Indonesia: richness and abundance. J Mar Biol Assoc UK 2004; 84(3): 581-91.

[15] Jackson JBC, Buss L. Allelopathy and spatial competition among coral reef invertebrates. Proc Natl Acad Sci USA 1975; 72: 5160-3.

[16] Ilan M, Abelson A. The life of a sponge in a sandy lagoon. Biol Bull 1995; 189: 363-9.

[17] Hoffmann F, Larsen O, Rapp HT, Osinga R. Oxygen dynamics in choanosomal sponge explants. Mar Biol Res 2005; 1(2): 160-3.

[18] Gerrodette T, Flechsig AO. Sediment-induced reduction in the pumping rate of the tropical sponge Verongia-Lacunosa. Mar Biol 1979; 55(2): 103-10.

[19] Tompkins-MacDonald GJ, Leys SP. Glass sponges arrest pumping in response to sediment: implications for the physiology of the hexactinellid conduction system. Mar Biol 2008; 154(6): 973-84.

[20] Bell JJ. Evidence for morphology-induced sediment settlement prevention on the tubular sponge *Haliclona urceolus*. Mar Biol 2004; 146(1): 29-38.

[21] Bell JJ, Barnes DKA. The distribution and prevalence of sponges in relation to environmental gradients within a temperate sea lough: Vertical cliff surfaces. Divers Distrib 2000; 6(6): 283-303.

[22] Carballo JL. Effect of natural sedimentation on the structure of tropical rocky sponge assemblages. Ecoscience 2006; 13(1): 119-30.

[23] Reiswig HM. *In-situ* pumping activities of tropical Demospongiae. Mar Biol 1971; 9(1): 38-50.

[24] Reiswig HM. Water transport, respiration and energetics of three tropical marine sponges. J Exp Mar Biol Ecol 1974; 14: 231-49.

[25] Sultan SAR, Ahmad F. Flushing of a coastal lagoon in the Red sea. Estuar Coast Shelf Sci 1990; 31(3): 345-9.
[26] Clarke KR, Gorley RN. Primer v6: User manual/tutorial. PRIMER-E Ltd: Plymouth United Kingdom 2006.
[27] Anderson MJ. A new method for non-parametric multivariate analysis of variance. Austral Ecol 2001; 26: 32-46.
[28] Clarke KR, Chapman MG, Somerfield PJ, Needham HR. Dispersion-based weighting of species counts in assemblage analyses. Mar Ecol Prog Ser 2006; 320: 11-27.
[29] Ayling AL. Patterns of sexuality, asexual reproduction and recruitment in some subtidal marine Demospongiae. Biol Bull 1980; 158(3): 271-82.
[30] Anderson MJ, Gorley RN, Clarke KR. PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E Plymouth: United Kingdom 2008.
[31] Roberts DE, Davis AR. Patterns in Sponge (Porifera) assemblages on temperate coastal reefs off Sydney, Australia. Mar Freshw Res 1996; 47(7): 897-906.
[32] de Voogd NJ, Cleary DFR. Relating species traits to environmental variables in Indonesian coral reef sponge assemblages. Mar Freshw Res 2007; 58(3): 240-9.
[33] Fraser SB, Sedberry GR. Reef morphology and invertebrate distribution at continental shelf edge reefs in the South Atlantic Bight. Southeast Nat 2008; 7(2): 191-206.
[34] Wilkinson CR, Cheshire AC. Patterns in the distribution of sponge populations across the Central Great Barrier Reef. Coral Reefs 1989; 8(3): 127-34.
[35] Bell JJ, Barnes DKA. The distribution and prevalence of sponges in relation to environmental gradients within a temperate sea lough: Inclined cliff surfaces. Divers Distrib 2000; 6(6): 305-23.
[36] Auster PJ. A conceptual model of the impacts of fishing gear on the integrity of fish habitats. Conserv Biol 1998; 12(6): 1198-203.
[37] Auster PJ, Langton RW. The effects of fishing on fish habitat. Fish Habitat: Essent Fish Habit Rehabil 1998; 22: 150-87.
[38] Rosenberg R. Effects of dredging operations on estuarine benthic macrofauna. Mar Pollut Bull 1977; 8(5): 102-4.
[39] Wassenberg TJ, Dews G, Cook SD. The impact of fish trawls on megabenthos (sponges) on the north-west shelf of Australia. Fish Res 2002; 58(2): 141-51.
[40] Jones JB. Environmental impact of trawling on the seabed: a review. N Z J Mar Freshwat Res 1992; 26: 59-67.
[41] Hiddink JG, Jennings S, Kaiser MJ, Queiros AM, Duplisea DE, Piet GJ. Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. Can J Fish Aquat Sci 2006; 63(4): 721-36.
[42] Done TJ, Potts DC. Influences of habitat and natural disturbances on contributions of massive *Porites* corals to reef communities. Mar Biol 1992; 114: 479-93.

Received: June 01, 2009 Revised: November 21, 2009 Accepted: January 05, 2010