RESEARCH ARTICLE

# Frequency of sublethal injury in a deepwater ophiuroid, *Ophiacantha bidentata*, an important component of western Atlantic *Lophelia* reef communities

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**Abstract** The occurrence and relative abundance of tissue (arm) regeneration in the ophiuroid, *Ophiacantha bidentata* (Retzius), was examined in individuals collected primarily among colonies of the deep-water coral *Lophelia pertusa* off the southeastern United States. Seven deep-water coral sites (384–756 m), located between Cape Lookout, NC, and Cape Canaveral, FL, were sampled in June 2004 using a manned submersible. The presence of regenerative tissue was evaluated by visual inspection of each individual ophiuroid, and the proportion of regenerating arms per individual was examined relative to size of individual, geographic location, and depth of collection. *Ophiacantha bidentata*, the dominant brittle star collected, commonly displayed signs of sublethal injury with over 60% of individuals displaying some evidence of regeneration. These levels of regeneration rival those reported for shallow-water ophiuroids. Larger individuals (>6.5 mm disc size) had a higher incidence of regeneration than smaller individuals. Size of individual and percent of regeneration were negatively correlated with depth. Although *O. bidentata* was significantly less abundant in southern versus northern sites, ophiuroid abundance did not appear to be influenced by amount or density of coral substratum. Presence of dense aggregations of *O. bidentata* indicates that they are an important component of the invertebrate assemblage associated with deep-water coral habitat especially in the northern part of the study area. Assuming that observed frequencies of injury and subsequent regeneration represent predation events then dense ophiuroid aggregations in deep-water coral habitats represent an important renewable trophic resource within these communities.

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## Introduction

Ophiuroids are common components of deep-sea benthic communities (e.g., Tyler 1980; Summers and Nybakken 2000; Metaxas and Giffin 2004). In diverse outer shelf and slope benthic habitats, ranging from low-profile, featureless sandy substrata to high-profile, coral habitats, ophiuroids can be extremely abundant, with hundreds to thousands of individuals occurring in aggregations (Grange 1991; Jensen and Frederiksen 1992; Piepenburg and Schmid 1996; Summers and Nybakken 2000; Metaxas and Giffin 2004). In some coral habitats ophiuroids may constitute a major component of the macrofauna utilizing interstitial spaces provided by deep-sea anthozoan colonies.

Where dense aggregations occur, ophiuroids provide an important link in trophic dynamics of deep-sea communities (Pearson and Gage 1984; Pomory and Lawrence 2001; Stancyk et al. 1994a; Summers and Nybakken 2000). Most ophiuroids are omnivorous, feeding on detritus, suspended organic material, small epifauna, and infaunal organisms. Some species display considerable trophic flexibility and are not restricted to one feeding mode. For example, *Ophiacantha bidentata* can switch from deposit-feeding to suspension-feeding, depending upon resource availability (Litvinova 1980; Gallagher et al. 1998). Such flexibility in feeding modes provides a conduit for transfer of energy between pelagic and benthic environments. Thus, these organisms play an important role in energy flow and secondary production through the utilization, processing, and redistribution of organic matter and subsequent transfer of organic material to higher trophic levels (Pearson and Gage 1984; Pape-Lindstrom et al. 1997; Summers and Nybakken 2000).

Ophiuroids tolerate a high level of sublethal injury in terms of arm or partial disc loss (Lawrence and Vasquez 1996; Sköld and Rosenberg 1996; Makra and Keegan 1999). The few studies concerning arm regeneration in deep-sea ophiuroids reported highly variable rates ranging from <3.8% for *Ophiacantha abyssicola* (Metaxas and Giffin 2004) to 98% for *Ophiura sarsi* (Stancyk et al. 1994b). Predation is the most commonly cited cause of such injuries to ophiuroids (e.g., Stewart 1996; Pape-Lindstrom et al. 1997), but physical stress (Woodley et al. 1981; Makra and Keegan 1999) has also been documented as an important causative agent of these injuries. Food resource levels (Clements et al. 1988; Lawrence and Vasquez 1996), water chemistry parameters (Donachy and Watabe 1986; Nilsson and Sköld 1996; Talbot and Lawrence 2000) and habitat type (Sides 1987; Aronson 1989; Clements et al. 1994; Rose 1997; Pomory and Lawrence 2001) can also influence injury rates and/or regeneration times.

*Ophiacantha bidentata* is broadly distributed in the western Atlantic, ranging from Greenland to central Florida at depths of 32–4730 m (Paterson 1985; this study). This species is a major component of the benthic invertebrate assemblage associated with deep-water coral reefs occurring off the southeastern United States (Nizinski et al., unpublished data) and commonly co-occurs with deep-water coral colonies, in particular, the azooxanthellate coral *Lophelia pertusa* (Tyler 1980; personal observation). In fact, study sites off North Carolina, characterized by monotypic stands of *L. pertusa*, are inhabited by large aggregations of this species (Nizinski et al., unpublished data). Dense aggregations of ophiuroids are rare in bathyal and abyssal environments (Metaxas and Giffin 2004) and particularly so for those species found in close association with deep-water corals.

Although mentioned in several studies (Tyler and Gage 1982; Pearson and Gage 1984; Paterson 1985; Piepenburg and Schmid 1996; Piepenburg et al. 1997; Gallagher et al. 1998), there is still relatively little known about the biology, ecology, and distribution of *O. bidentata*; frequencies of sublethal injury and subsequent regeneration rates are unknown for this species. Although predation pressure has been examined on some ophiuroid species that occur at high densities (e.g., Warner 1971; Aronson and Harms 1985; Aronson 1989; Munday 1993), fewer studies have investigated predation processes on deep-sea ophiuroids that form dense aggregations (e.g., Metaxas and Giffin 2004). Since *O. bidentata* was observed at both high and low densities, intraspecific comparisons of sublethal injuries relative to ophiuroid density and abundance were possible.

During surveys of deep-sea coral communities off the southeastern United States, individual *O. bidentata* were observed and sampled in-situ. Using a manned submersible to collect individuals allowed recovery of more undamaged individuals than would be possible using more conventional means (i.e., dredge or trawl). Objectives of this study were to: (1) determine the presence/absence, and relative abundance of tissue (arm) regeneration among individuals from the observed ophiuroid aggregations, (2) describe differences in the proportion of arm regeneration relative to individual disc size, and (3) compare the amount of arm regeneration observed in *O. bidentata* to that of other ophiuroids.

## Materials and methods

### Study sites

Seven deep-water coral sites, located between Cape Lookout, NC and Cape Canaveral, FL, were sampled during dives at each site with the manned submersible Johnson-Sea-Link (JSL) from 12 to 21 June 2004 (Table 1). Live coral, dead coral, and coral rubble were the predominant substrata surveyed at each site. Our preliminary observations indicated some geographic habitat differences that could influence our analyses. North of about 33°N, coral mounds are large and dominated by *L. pertusa*, with other corals being poorly represented. South of about 33°N, coral diversity increases and corals are attached to other hard substrata as well as occurring on mounds that may be lithoherms or bioherms (Reed 2002). Other scleractinian species (e.g., *Enallopsammia profunda*, and *Madrepora oculata*), soft corals and sponges also become more prevalent south of 33°N. Given these general regional differences in benthic habitats and the small number of replicate sites, we pooled sites into northern (=North Carolina) versus southern (South Carolina to Florida) sites to test for geographic differences in some analyses.

**Table 1** Study sites off the southeastern US where submersible based observations and coral collections containing ophiuroids were made, 12–21 June 2004

| Site | Date | Latitude | Longitude | Depth (m) | No. of individuals | Mean disk diameter (SE) | Mean no. of arms present (SE) | Mean no. of arms regenerating (SE) | Mean percent of arms regenerating (SE) |
|---|---|---|---|---|---|---|---|---|---|
| JSL-04-4688 | 6/12/2004 | 31°46.45 | 79°11.70 | 516–531 | 24 | 6.8 (±0.3) | 4.3 (±0.3) | 1.8 (±0.3) | 38.5 (±6.6) |
| JSL-04-4692 | 6/15/2004 | 34°19.42 | 75°47.17 | 384–425 | 147 | 6.4 (±0.1) | 4.1 (±0.1) | 1.2 (±0.1) | 32.5 (±3.0) |
| JSL-04-4693 | 6/15/2004 | 34°19.44 | 75°47.14 | 431 | 107 | 6.6 (±0.1) | 4.3 (±0.1) | 1.3 (±0.2) | 28.9 (±3.2) |
| JSL-04-4694 | 6/16/2004 | 34°11.28 | 75°53.61 | 396–440 | 21 | 7.2 (±0.2) | 4.3 (±0.2) | 1.1 (±0.3) | 24.1 (±5.9) |
| JSL-04-4695 | 6/16/2004 | 34°11.41 | 75°53.65 | 414–442 | 13 | 6.7 (±0.2) | 4.0 (±0.3) | 1.5 (±0.5) | 34.5 (±11.0) |
| JSL-04-4696 | 6/17/2004 | 33°34.37 | 76°27.71 | 390–402 | 109 | 6.3 (±0.1) | 4.3 (±0.1) | 1.8 (±0.2) | 39.8 (±3.2) |
| JSL-04-4697 | 6/17/2004 | 33°34.57 | 76°27.83 | 405–411 | 5 | 5.6 (±0.8) | 3.6 (±0.8) | 1.0 (±0.5) | 43.3 (±19.4) |
| JSL-04-4698 | 6/18/2004 | 31°49.45 | 77°36.69 | 663–703 | 10 | 5.0 (±0.3) | 3.5 (±0.4) | 0.4 (±0.2) | 9.8 (±5.1) |
| JSL-04-4699 | 6/18/2004 | 31°50.89 | 77°36.72 | 660–696 | 2 | 3.3 (±1.0) | 4.0 (±1.0) | 0.0 (±0.0) | 0.0 (±0.0) |
| JSL-04-4701 | 6/19/2004 | 30°28.94 | 79°38.50 | 647–674 | 2 | 4.7 (±1.6) | 3.5 (±0.5) | 0.0 (±0.0) | 0.0 (±0.0) |
| JSL-04-4702 | 6/20/2004 | 28°47.70 | 79°37.40 | 713–738 | 3 | 5.8 (±0.4) | 4.3 (±0.7) | 2.7 (±0.4) | 62.2 (±2.2) |
| JSL-04-4703 | 6/20/2004 | 28°46.62 | 79°36.96 | 742–756 | 2 | 4.0 (±0.6) | 5.0 (±0.0) | 1.5 (±1.5) | 25.0 (±25.1) |
| JSL-04-4704 | 6/21/2004 | 28°02.64 | 79°36.82 | 738–739 | 9 | 3.7 (±0.4) | 4.7 (±0.2) | 0.9 (±0.3) | 20.7 (±8.0) |

Mean disk size and occurrence of arm regeneration per individual *Ophiacantha bidentata* collected. The category of number of arms present includes both intact and regenerating arms

## Field sampling and specimen treatment

During each dive, megafaunal samples were collected opportunistically. Most ophiuroid specimens were collected during discrete sampling of live coral segments or coral rubble and placed in individual buckets using either the JSL suction sampler or manipulator arm claw. All ophiuroids were carefully separated from the collected coral material using forceps to ensure that arms were not damaged. Disc size was measured to the nearest 0.1 mm using dial calipers, following methods similar to those of Metaxas and Giffin (2004). Number of complete arms (i.e., full arm present, showing no obvious external signs of regeneration from disc to tip) and regenerating arms (arm showing discontinuity in thickness; Bowmer and Keegan 1983; Munday 1993) were counted for each individual. The proportion of regenerating arms per individual was calculated by dividing the number of arms displaying regeneration by the total number of arms (complete + regenerating arms) present. If an arm was missing or broken without the presence of regenerated tissue or scars, it was excluded from analyses because we were uncertain whether the damage was incurred during sampling. Thus, our estimates of sublethal injury and subsequent regeneration were conservative.

## Statistics

The response variables of ophiuroid size and percent of regenerating arms per individual were analyzed among locations (independent variable) using the non-parametric Kruskal–Wallis ANOVA since data were not normally distributed. Significant differences were examined further using Dunn's multiple comparisons. Spearman Rank Order Correlations were calculated to determine significant relationships between ophiuroid size and study site depth, and between ophiuroid size and percent of regenerating arms per individual. Additionally, both ophiuroid size and percent of regenerating arms per individual were pooled for sites off North Carolina (northern sites, north of latitude: 33°30′N) and for all sites south of 33°30′N (southern sites). These two groups were then analyzed using a Mann–Whitney Rank Sum test. These pooled data were also analyzed to test for northern versus southern site differences in proportion of regenerating individuals and proportion of individuals regenerating a specific number of arms using a $Z$ test and Chi-square test, respectively.

## Results

*Ophiacantha bidentata* was the numerically dominant ophiuroid ($N = 454$) collected throughout the study area, constituting 90% of individuals sampled. The largest aggregations of this species with densities ranging from 100s to 1,000s of individuals m$^{-2}$ (Nizinski et al., unpublished data) were observed at study sites off North Carolina. At the northern sites, individuals were observed and collected during 100% of submersible dives. At southern sites, *O. bidentata* densities tended to be an order of magnitude less (10 individuals m$^{-2}$; Nizinski et al., unpublished data) and individuals were collected only during 41% of dives.

Individual *O. bidentata* ranged in size from 2.2 to 11.1 mm disc diameter. Ophiuroid size differed by both location and depth. Mean disc size differed significantly among sites (Kruskal–Wallis; $P = 0.001$; Fig. 1a, Table 1). No pair-wise comparisons between sites, however, were significant (Dunn's Multiple Comparisons; $P = 0.05$) probably due to small sample sizes overall and low abundances at the southernmost sites. When data were separately pooled for northern and southern sites, mean disc size of individuals from southern sites ($\bar{x} = 5.5$ mm) was significantly smaller than that for individuals from more northern sites ($\bar{x} = 6.4$ mm; Mann–Whitney Rank Sum; $P = 0.001$). Among three northern sites, the only sites where more than 100 individuals were collected, size frequency distributions were similar (Fig. 2); a broad size range was represented with the majority of individuals between 6 and 7.5 mm disc diameter. Mean disc size of individual *O. bidentata* was negatively correlated with water depth (Spearman Rank Order Correlation; $r = –0.7$; $P = 0.01$; Fig. 1b) with larger individuals occurring at shallower depths (390–531 m) than smaller individuals (647–756 m). Thus, larger individuals were generally observed at the northern, shallower sites.

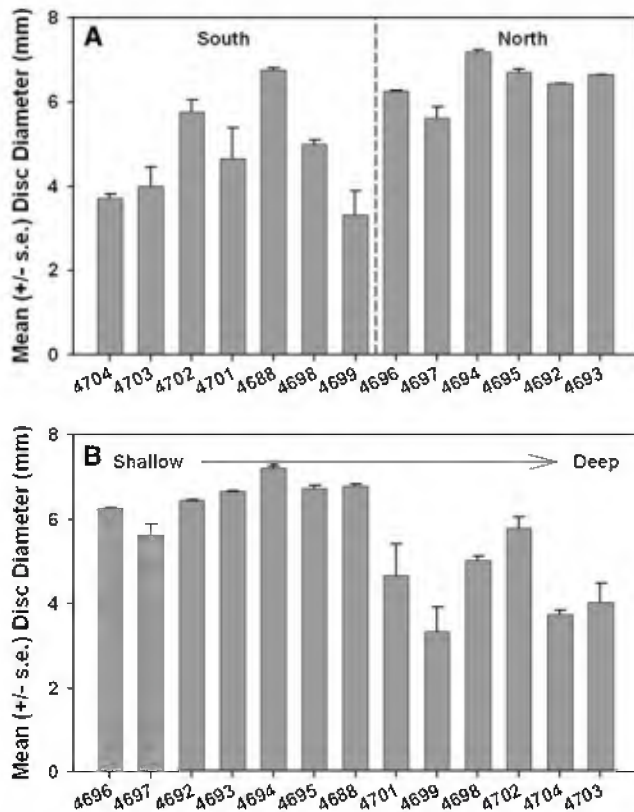Many individuals of *O. bidentata* exhibited a relatively high incidence of sublethal injury as evidenced by tissue



**Fig. 2** *Ophiacantha bidentata.* Size frequency distribution by site for those sites where more than 100 individuals were collected



**Fig. 1** *Ophiacantha bidentata.* Relationship between mean disk size and **a** geographic location and **b** depth. See Table 1 for details on sample size, site locations, and depth
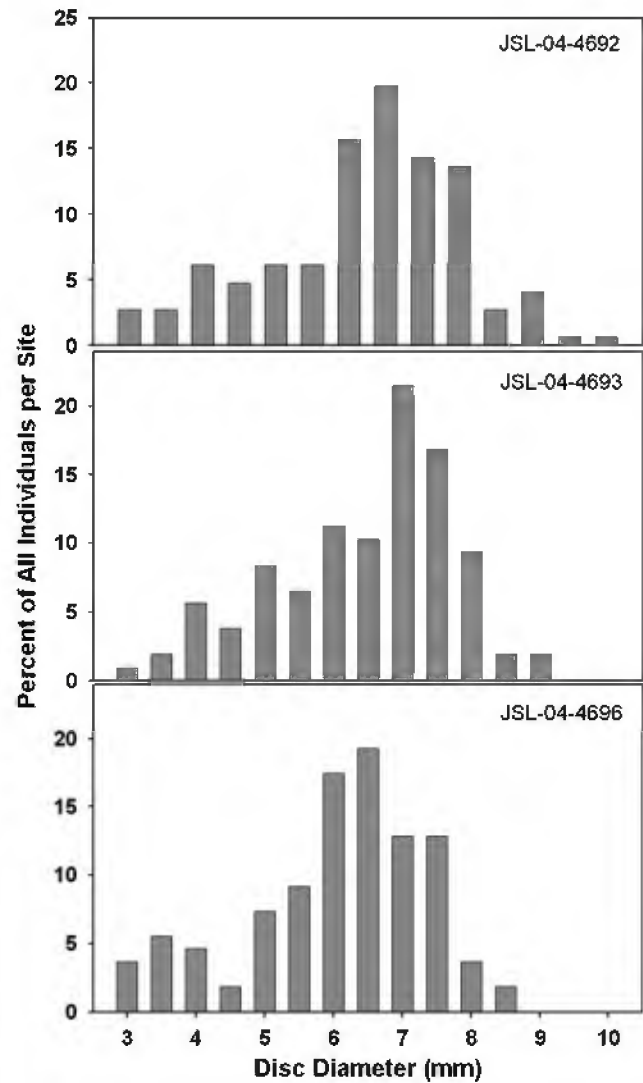
regeneration. Overall, 60% of individuals and $32.6 \pm 1.6\%$ of arms showed signs of regeneration. Number of arms regenerating on a single individual ranged from 1 to 5. Of individuals possessing five arms total (including both complete and regenerating arms), over 35% of individuals were repairing either one or two arms; 9.6% had all five arms undergoing regeneration (Fig. 3a). When all individuals were considered, regardless of the number of arms present at the time of collection, a similar pattern was found with over 38% of individuals repairing either one or two arms; over 5% of the total sample population had all arms undergoing regeneration (Fig. 3b). Mean percentage of regenerating arms per individual per site ranged from 0 to 62% (Table 1). Size of individual ophiuroids and percentage of arms undergoing regeneration were positively correlated (Spearman Rank Order Correlation; $r = 0.11$; $P = 0.02$; Fig. 4). Larger individuals (>6.5 mm
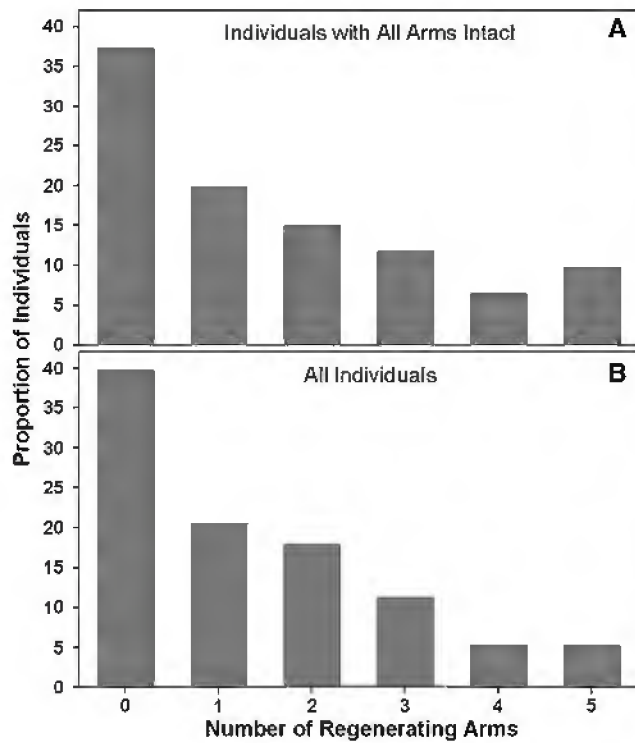
Fig. 3 *Ophiacantha bidentata*. **a** Proportion of individuals possessing five arms at time of sampling that were observed regenerating 1–5 arms; **b** proportion of individuals, regardless of number of arms present at time of sampling, observed regenerating 0–5 arms
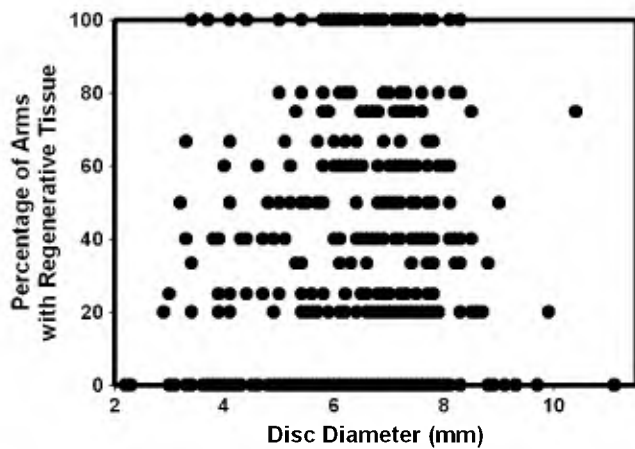


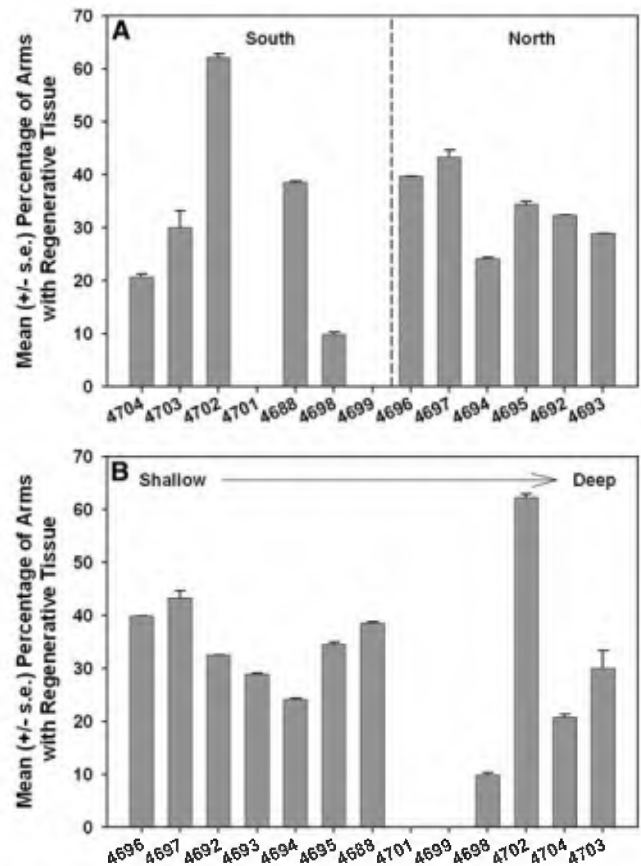Fig. 4 *Ophiacantha bidentata*. Relationship between percentage of arms regenerating and disc size



Fig. 5 *Ophiacantha bidentata*. Relationship between mean percentage of arms with regenerative tissue and **a** geographic location and **b** depth. See Table 1 for details on sample size, site locations, and depth

disc diameter) had a higher incidence of regeneration than did smaller individuals ($35.4 \pm 2.2$ vs. $29.8 \pm 2.3\%$ of arms, respectively).

The percent of *O. bidentata* with arms regenerating was significantly different among sites (Kruskal–Wallis; $P = 0.03$; Fig. 5a). Likely for the same reasons given above, no pair-wise comparisons were significant (Dunn's Multiple Comparisons; $P = 0.05$). When data were separately pooled

for northern and southern sites, percentage of regenerating arms was not significantly different for *O. bidentata* between northern and southern sites (Mann–Whitney Rank Sum; $P = 0.39$). Also the proportion of individuals undergoing regeneration was not significantly different between these sites ($Z$ test; $P = 0.57$). Additionally, the proportion of individuals regenerating a specific number of arms (i.e., 1–5 arms) did not differ significantly between northern and southern sites (Chi-square; $X = 4.46$; $P = 0.35$). Although percent of regenerating arms per individual was not correlated with depth (Spearman Rank Order Correlation; $r = -0.3$; $P = 0.24$; Fig. 5b), a slight negative trend was evident in these data. Mean percentage of arms with regenerative tissue varied from 24 to 43% at shallower sites and 0–62% at deeper sites.

## Discussion

Sublethal injury undoubtedly has a substantial effect on the biology and ecology of ophiuroids. While regenerating, ophiuroids incur direct energy costs to replace lost biomass. For example, an estimated 14–19% of total organic

production can be spent on regeneration of body parts in some ophiuroids (Singletary in Lawrence and Vasquez 1996). Indirect costs of sublethal injuries involve the loss of function, such as restricted movement capabilities and decreased ability to feed (Lawrence and Vasquez 1996).

Frequency of sublethal injury and subsequent regeneration of injured or lost arms may be influenced by the population density of the ophiuroid species. *Ophiacantha bidentata* occurred in high densities, particularly at the northern sites, and the proportion of individuals undergoing regeneration from these dense aggregations was much higher than that reported for other species that form aggregations. For example, Aronson (1989) reported a relatively low incidence of injury for shallow-water ophiuroids (*Ophiothrix fragilis* and *Ophiocomina nigra*) that form dense aggregations (>2,000 individuals m⁻²) and suggested decreased predator-prey encounter rates may explain this. Alternatively, whole-organism capture or diminished predator efficiency due to the high population density was hypothesized to explain the low incidence of regeneration observed in *Ophiacantha abyssicola*, a species that occurs in dense aggregations on the continental slope (430–498 m) off Nova Scotia (Metaxas and Giffin 2004). In contrast, low predation rates accompanied by slow regeneration rates (years) are hypothesized for the high incidence of sublethal injury reported for *Ophiura sarsi* (Stancyk et al. 1994b). Whether aggregation density influences the degree of injury in the *O. bidentata* that we observed requires additional study.

Habitat structure can also influence the amount of injury incurred by ophiuroids either by attracting predators or providing protection to ophiuroids from their predators. For example, based on results of experiments utilizing tethered individuals, ophiuroids inhabiting rocky reef sites in the British Isles incurred higher per capita injury levels and significantly higher mortality than those occurring in dense aggregations on a pebble, shell, and sandy silt substratum (Aronson 1989). Aronson hypothesized that this difference in mortality rate (death or disappearance) was due to fast moving, efficient predators, which were more common at rocky reefs than on the ophiuroid beds. Conversely, lower frequencies of injury (18 vs. 47%) were reported for *Ophiocoma echinata* inhabiting densely packed rock rubble at Pigeon Key, FL, which presumably offered better protection from predators (Pomory and Lawrence 2001). The proportion of individuals of *O. bidentata* with regenerative tissue occurring on the *Lophelia* reefs and in the *Lophelia* rubble is high (60%) compared with the range of values (18–92%; Sides 1987; Aronson 1989; Pomory and Lawrence 2001) reported for ophiuroids inhabiting rocky reef and rubble habitats.

Behavior, perhaps influenced by habitat type, may play a role in the magnitude of injuries exhibited in ophiuroids. In this study, individual *O. bidentata* were observed with arms intertwined within the coral-branch matrix, a posture that might shelter them partially from predators or make it more difficult for a predator to remove the entire ophiuroid during an attack. Here, in contrast to other species where dense aggregations forming mats obscure individuals, individual *O. bidentata* were recognizable and distal portions of their arms were observed protruding from the coral matrix. An advantage to living in the coral matrix may be that, even though arms are at risk, whole organism capture and extraction are likely more difficult. Additionally, this species exhibits bioluminescence (Herring 1974). Luminescence in *O. bidentata* may reduce mortality via predation but, in turn, could enhance the likelihood of sublethal injury. In some ophiuroids, bioluminescence is considered a defense mechanism that may allow the individual to avoid being totally consumed by a predator (e.g., Basch 1988; Herring 1995). Instead, the luminescent arms may lure the predator towards the arms and away from the body, and the arms are then sacrificed either by predator consumption or through autonomy (Basch 1988; Deheyn et al. 2000; Mallefet et al. 2001).

Incidence of sublethal injury and subsequent regeneration was correlated with size of the ophiuroid; larger *O. bidentata* exhibited higher occurrences of regeneration. Higher incidence of sublethal injury in larger individuals has also been reported in other ophiuroids (Munday 1993; Sköld and Rosenberg 1996). If larger size indicates older individuals (rather than just faster growth), the possibility of receiving an injury increases with time (Sköld and Rosenberg 1996). Additionally, larger individuals may have longer arms, and therefore, may be more conspicuous and more susceptible to cropping by predators.

Frequency of sublethal injury reported for both deep- and shallow-water ophiuroid species is highly variable, ranging from <4 to 98% and 20% to almost 100%, respectively (Stancyk et al. 1994b; see review in Lawrence and Vasquez 1996; Pomory and Lawrence 2001, and references therein; Metaxas and Giffin 2004). The high incidence of regeneration (60%) observed for *O. bidentata* is in the mid-range of that reported for both deep- and shallow-water species. However, given such high levels of variability within and between groups of ophiuroids occurring in different depth zones, whether depth of occurrence is a factor in the frequency of injury observed in these ophiuroids is uncertain.

Feeding mode and the organism's relationship to the substratum (i.e., infauna, epifauna) also influence incidence of sublethal injury in ophiuroids. For example, infaunal suspension and deposit-feeding species of ophiuroids have significantly more scars per arm than do epibenthic suspension feeders or epibenthic carnivores and deposit feeders at sites off the Swedish west coast (Sköld and Rosenberg

1996). Also, burrowing amphiurid ophiuroids (e.g., *Microphiopholis gracillima*), which extend their arms to the surface to deposit or suspension feed, often lose portions of their arms to epibenthic predators (Pape-Lindstrom et al. 1997). Although *O. bidentata* is an epibenthic deposit/suspension feeder, the frequencies of sublethal injury observed were more similar to those of infaunal species than those observed in other epibenthic ophiuroids. This is not surprising given the similarities between the postures exhibited by *O. bidentata* intertwined within the *Lophelia* coral matrix and that reported for burrowing amphiurids.

In general, *O. bidentata* is a deep-sea, epifaunal, deposit/suspension feeder that occurs in dense aggregations in highly structured coral and coral rubble habitats. Large aggregations of ophiuroids in complex habitats would suggest a relatively low incidence of sublethal injury per individual; however, high frequencies of injuries were observed on individuals examined in this study. Although sublethal predation on ophiuroids is presumed to occur in many species, it has only rarely been documented (Lawrence and Vasquez 1996). The degree of injury observed in this study may not result entirely from predation; however, other factors known to cause sublethal injury in ophiuroids, such as wave energy and physical stress, should be minimal in the deep sea, making predation the more likely causative agent for these injuries. Such high levels of regeneration also suggest a higher degree of predation on these ophiuroids (or their body parts) compared with ophiuroids inhabiting other areas.

The high densities of *O. bidentata* on *Lophelia* reefs off the southeastern United States should be considered when estimating an energy budget for these deep-reef systems. Ophiuroid linkages in marine food webs have been documented and sublethal predation can be a significant pathway of secondary-production energy flow (Stancyk et al. 1994a; Gielazyn et al. 1999). Predation on ophiuroids by fishes, shrimps, polychaetes, asteroids, crabs, and other ophiuroids have been reported (Aronson 1987; Wassenberg and Hill 1987; Feder and Pearson 1988; Munday 1993; Pape-Lindstrom et al. 1997). Thus, if injuries reflect high levels of sublethal predation, then *O. bidentata* may provide a "renewable resource pool" (Stancyk et al. 1994a) to the deep-water *Lophelia* community that may otherwise be dependent upon exogenous sources of nutrients.

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