

Habitat utilization by macrobenthos in deep-sea sandy fields: examples from the An'ei Seamount, Izu-Ogasawara Arc

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Although sandy substrates are known to occupy a large proportion of oceanic seafloor, biological research on this system has been less intensive compared with that on biota associated with rocky substrates including sulphide deposits of hydrothermal vents. Macrobenthos inhabiting a deep-sea sandy field have a major problem to overcome, i.e., gaining a secure anchorage whilst getting access to food resources. It may be hypothesised that deposit-feeding and infaunal life styles are less suitable for macroinvertebrates inhabiting deep-sea sandy fields in comparison to their shallow water counterparts, as (i) sediment organic content tends to be low and (ii) supply of potential food particles into the sediment and on the sediment surface is less frequent in deep sea sandy fields. Conversely, this would lead to the predominance of epifaunal, suspension-feeding type of macrobenthos in these habitats. Unfortunately, at present there is not enough information on the faunas of deep-sea sandy fields to enable definite testing of this hypothesis. In recognition of such a situation, this article presents some qualitative data based on photographic records obtained from a survey of sandy fields at 1340-1480 m depth on the An'ei Seamount, Izu-Ogasawara Arc, in western Pacific. The fauna was dominated by diverse taxa of suspension-feeding, epifaunal Anthozoa, particularly octocorallians (most notably gorgonians); other taxa such as ophiuroids and galatheids were often observed in association with these anthozoans. Crinoids and crustaceans were also common. Four categories of habitat utilization have been recognised: (1) sessile life, being attached to inorganic substrates (rocks and stones) scattered on sandy fields; (2) sessile/commensal life, being attached to organic substrates (i.e., other sessile animals); (3) mobile life, relying upon hard substrates for suspension feeding; (4) mobile life, involving deposit feeding/scavenging. Consideration was given to an ability to live in sandy habitats as a potentially important element of evolutionary success for deep-sea macroinvertebrates which normally rely upon hard substrates.

Keywords : suspension feeding, octocorallians, gorgonians, galatheids, crinoids, commensals

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1. Introduction

Sandy fields predominate where current-generated energy is sufficiently strong to carry away silt-sized particles while allowing the deposition of sand particles on a low-gradient seafloor. With the presence of deep-sea currents flowing over large tracts of low gradient plains, it is natural that a large proportion of deep-sea beds has sandy substrates. However, research on deep sea sandy fields has been rather limited, partly because the (supposedly) low density of organisms in such environments makes data acquisition less efficient and attractive an undertaking and more costly in terms of the time invested in energy and manpower.

Among shallow-water macrobenthos inhabiting sandy substrates, two modes of feeding predominate: deposit feeding and suspension feeding (Little, 2000). The former relies on particulate organic matter deposited on the sediment surface, while the latter relies on essentially the same material (dead and/or living) suspended and carried by water currents. The existence of benthic boundary layer suggests that supply of organic particles close to the sediment surface is much reduced compared with some height above the surface (Gage and Tyler, 1991). While this may not be a problem in shallow waters where the absolute amount of suspended organic particles is large, the situation may be more critical in deeper waters where the density of organic particles in water is much reduced to start with and, consequently, even smaller quantities of particles would be deposited and become available on the sediment surface. This would in turn make deposit feeding less favourable an option among macrobenthos inhabiting sandy substrates in deep-seas. Further, as the infaunal mode of living generally involves either deposit feeding on/below the sediment surface or suspension feeding just above the surface, the problem of low supply of food also applies. Thus, it is possible to hypothesise that epifaunal life with suspension feeding is more likely to be adopted widely by macrobenthos inhabiting deep-sea sandy fields than infaunal life and deposit feeding. While there is a dearth of information to allow a formal test, it is considered worthwhile to examine data with reference to such a working hypothesis. With this in mind, the present article reports on the fauna of sandy fields on the An'ei Seamount (29°15'N, 138°37'E) in the Izu-Ogasawara Arc, western Pacific (Fig.1), focusing in par-

ticular on the aspects of habitat utilization by macroinvertebrates. Predominantly sandy fields with scattered volcanic stones and rocks occurred at 1340-1480 m depth on a gentle slope (average gradient = 5.2°) of this seamount (Fig. 1).

The data were obtained as video recordings and photographic images on board a manned submersible 'Shinkai 2000' in June 1999. Video recording was carried out continuously throughout a bottom cruise and stereo photographs were taken at intervals of 45-60 seconds. Still photographs were also taken from an observation port of the vehicle using a hand-held SLR camera, especially when the submersible was temporarily at rest on the seabed. Part of the results of this diving survey, dealing in particular with the spatial distribution of a deep-sea crinoid *Pentametrocrinus tuberculatus* (A.H. Clark) mainly on rocky substrates, was published elsewhere (Tokeshi 2002). This article focuses on the fauna of predominantly sandy fields.

2. Modes of habitat utilization in sandy fields

In deep-sea organisms suspension feeding can be achieved by adopting either (i) a mobile or free-ranging mode of life, or (ii) a sessile mode being attached to a substrate. In the former, a permanently nektonic existence is energetically untenable for most macroinvertebrates lacking the combination of body plan and metabolism that allows sustained maintenance of position in constantly moving bottom currents. Thus, organisms, although mobile, are largely dependent upon a substrate (and this includes both suspension feeders and deposit feeders). In the case of a sessile mode of life, because small sand particles do not provide a secure anchorage in a deep-sea sandy habitat where strong currents exist, macroinvertebrates need to find other, more stable substrates. In this respect, suspension feeders have to cope with two conflicting demands: a need to expose themselves to currents which carry food particles and to ensure that they themselves are not dislodged and carried away. Here, among macroinvertebrates inhabiting the sandy fields of the An'ei Seamount, four categories of habitat utilization have been recognised:

(type 1) sessile life, being attached to inorganic substrates (rocks and stones) scattered on sandy fields,

(type 2) sessile/commensal life, being attached to organic substrates (i.e., other sessile animals),

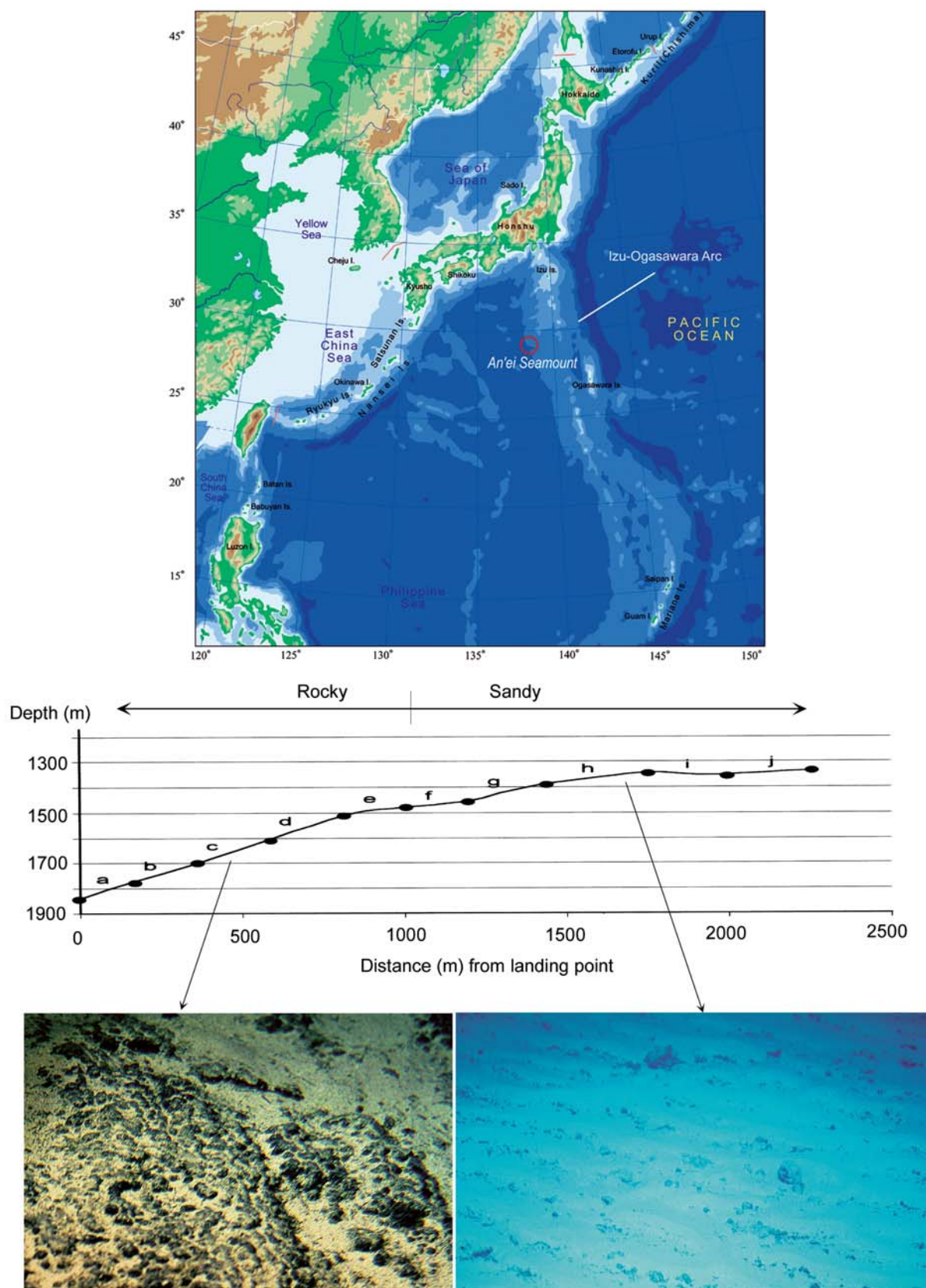


Fig. 1 Location of the An'ei Seamount on the Izu-Ogasawara Arc in western Pacific (upper panel), depth-profile of the cruising route (middle panel) where zones *a* to *e* were predominantly rocky and *f* to *j* predominantly sandy with scattered stones and rocks, the contrast being demonstrated in bottom photographs. Left photograph: lava rocks interspersed by sandy patches on a slope; rock morphology suggests that lava was cooled and solidified underwater. Right photograph: ripple marks are visible on a sandy field, suggesting the presence of a predominantly unidirectional current.

(type 3) mobile life, relying upon hard substrates for suspension feeding, and

(type 4) mobile life, involving deposit feeding/scavenging.

In the following section, macroinvertebrates recorded in this survey are described with reference to these types.

3. Macroinvertebrates of sandy fields on the An'ei Seamount

Octocorallians, gorgonians in particular, represented the most important suspension-feeding fauna (type 1 in the previous section) in the sandy fields of An'ei Seamount. Their existence depended on the presence of volcanic rocks which were scattered on the sandy field; interestingly, these organisms were not observed on predominantly rocky slopes between 1840–1480 m depth (zones a–d in Fig. 1).

Using scattered, often small, hard substrates as an anchoring point, gorgonians maintained an upright position with polyp-bearing branches being exposed to currents. For example, *Callogorgia flabellum* (Ehrenberg) with its expanded upper branches was commonly observed in this habitat (Fig. 2a) with its base securely cemented onto a rock surface (Fig. 2b). It is notable that its *in situ* posture on the seabed (Fig. 2a) was accurately preserved in the shape of the collected specimen (Fig. 2c). Another notable point is the occurrence of an ophiuroid *Asteronyx loveni* Müller et Troschel whose arms (the longest = 37 cm) were securely twisted around different branches of *Callogorgia*, its position on the gorgonian being little changed in the collected, dead specimen (note the position of the disc in Figs 2a and d; two photographs were taken from opposite directions). The photographs apparently show that the ophiuroid was positioned with its buccal side facing *Callogorgia*'s body. This ophiuroid species has long been known from deep waters, but there is a paucity of information on its *in situ* mode of life. Apparently, there seems no harm being inflicted upon *Callogorgia* by *A. loveni*, suggesting that the ophiuroid uses the gorgonian as obligate 'substrate' or host (type 2) for suspension feeding. Considering the difficulty of reaching another host across a barren, current-exposed field, it is most likely that individuals of this ophiuroid species become virtually sessile (as many other physically-mobile species probably are), once they settle as juveniles on a suitable

gorgonian host.

Another example of the primary substrate user and its commensal is shown in Fig. 3. An unidentified gorgonian (?) species occurred on a sandy slope with the base of its elongated stalk (ca. 50 cm in length) attached onto a half-buried rock. The polyp-bearing top part is maximally exposed to the current by a slight bending of the stem. An ophiuroid, probably *A. loveni*, was again attached onto this sessile host (i.e. type 2 on type 1). It is notable that this ophiuroid was also attached to the central part of the host's body, as in the previous example, that provides the securest anchorage. Fig 3c shows another example of octocorallian with its polyps positioned high up on an elongated, flexible stalk.

Fig. 4 shows a peculiar case of a sessile, suspension feeding octocorallian (gorgonian ?) and its commensal, a galatheid crab. This unidentified octocorallian has a main stem bending in a three-dimensional, helicoidal spiral with regular branching and polyps borne at regular intervals (Fig. 4a). As branch length gradually increases from base upwards and then decreases acutely to the tip, the specimen has a leaf-shape in its side view. These morphological characteristics suggest that this is a fully-grown colony; colonies of similar sizes were also observed in the field, standing upright on scattered rock surfaces (Fig. 4b). Another remarkable aspect of this 'Christmas-tree' octocorallian is its commensal, a galatheid (Fig. 4b–d). The crab was anchored to the host's branches with its extended legs; this association was observed a number of times during the diving survey. The morphology of this galatheid, i.e. its elongated legs and sharply-bending claws, appeared not an accidental coincidence for a commensal life on this host. It may be speculated that this crab is a deposit feeder/scavenger that relies on the host as a food trap+refugia (type 4 on type 1), but naturally this awaits further confirmation.

Rock islands are used by a variety of organisms, often presenting a situation which may be aptly described as 'oasis' where different species share limited space (Fig 5). On a stone surface measuring about 20 cm across, at least three suspension feeders and two deposit feeders/scavengers occurred (Fig. 5a). The suspension feeders, two actinians (one large and the other small) and one pennatulacean, were apparently positioned such that their tentacles do not interfere with each other. It is

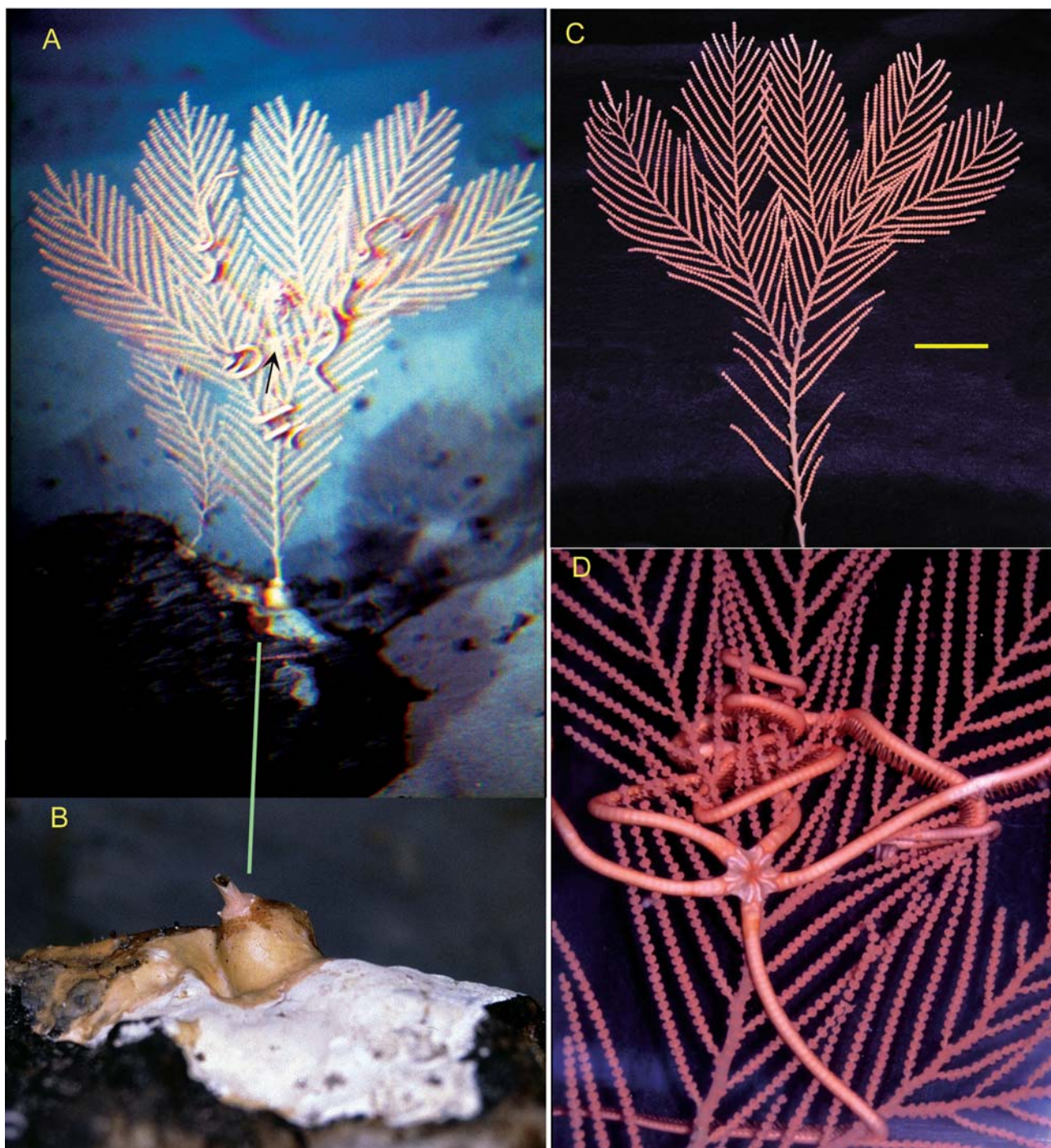


Fig. 2 (a) *In situ* photograph of *Callogorgia flabellum* with the ophiuroid *Asteronyx loveni* attached at 1477 m depth. The position of the ophiuroid's disc (on the other side of *Callogorgia*) is indicated by an arrow. (b) Detail of a basal cement (white and cream-coloured) of *Callogorgia*. (c) Collected specimen of *Callogorgia*. Scale bar = 5 cm. Note that some lower branches were lost when grabbed by the submersible's manipulator at the time of sampling. (d) Details of the attached *Asteronyx loveni* on *Callogorgia*.

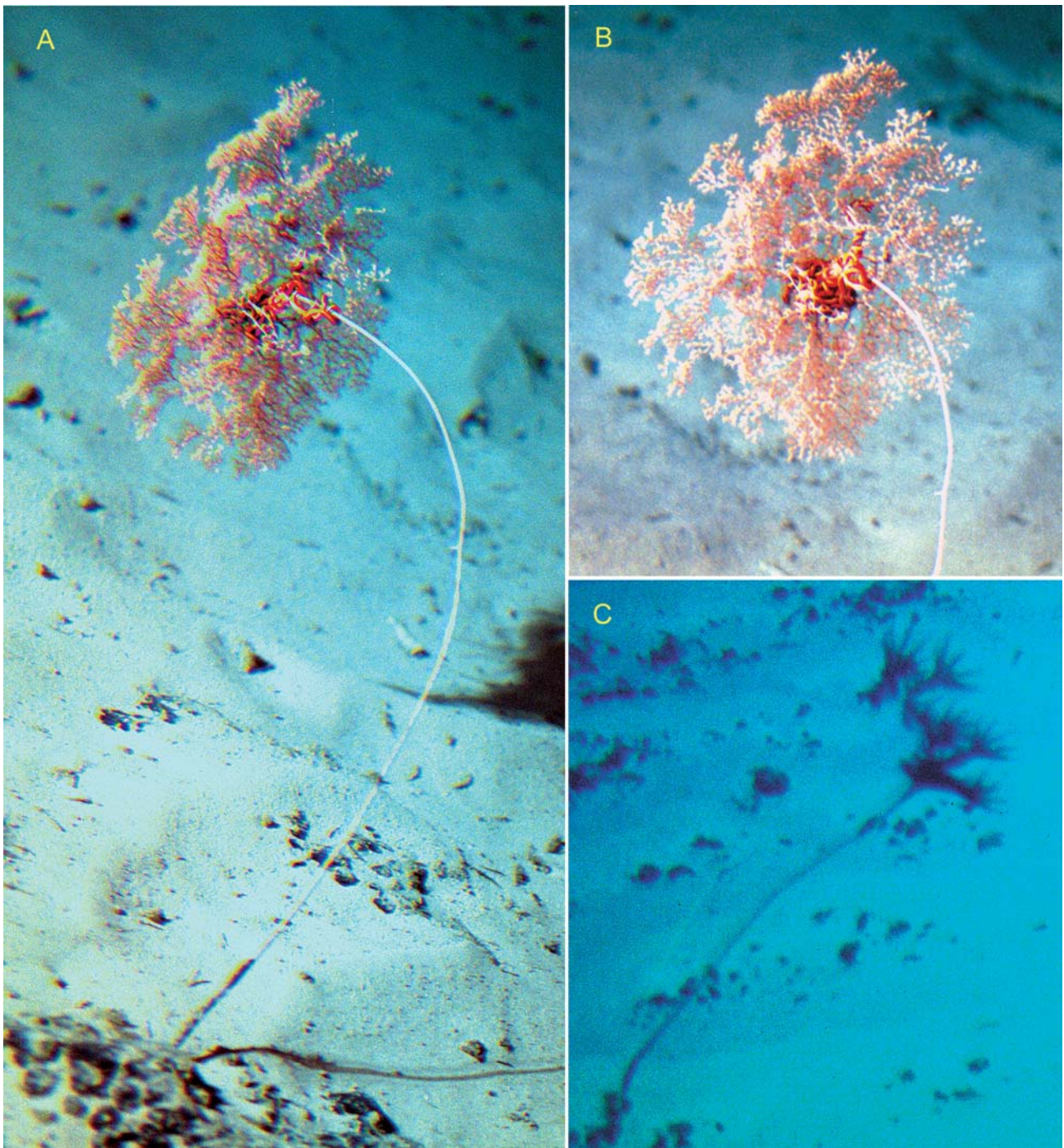


Fig. 3 (a)-(c) Stalked octocorallians (gorgonians) on a sandy slope of the An'ei Seamount, at 1343 m depth. An ophiuroid is attached in (a) and (b), photographs taken at two separate moments (note the difference in coiling pattern of the ophiuroid).

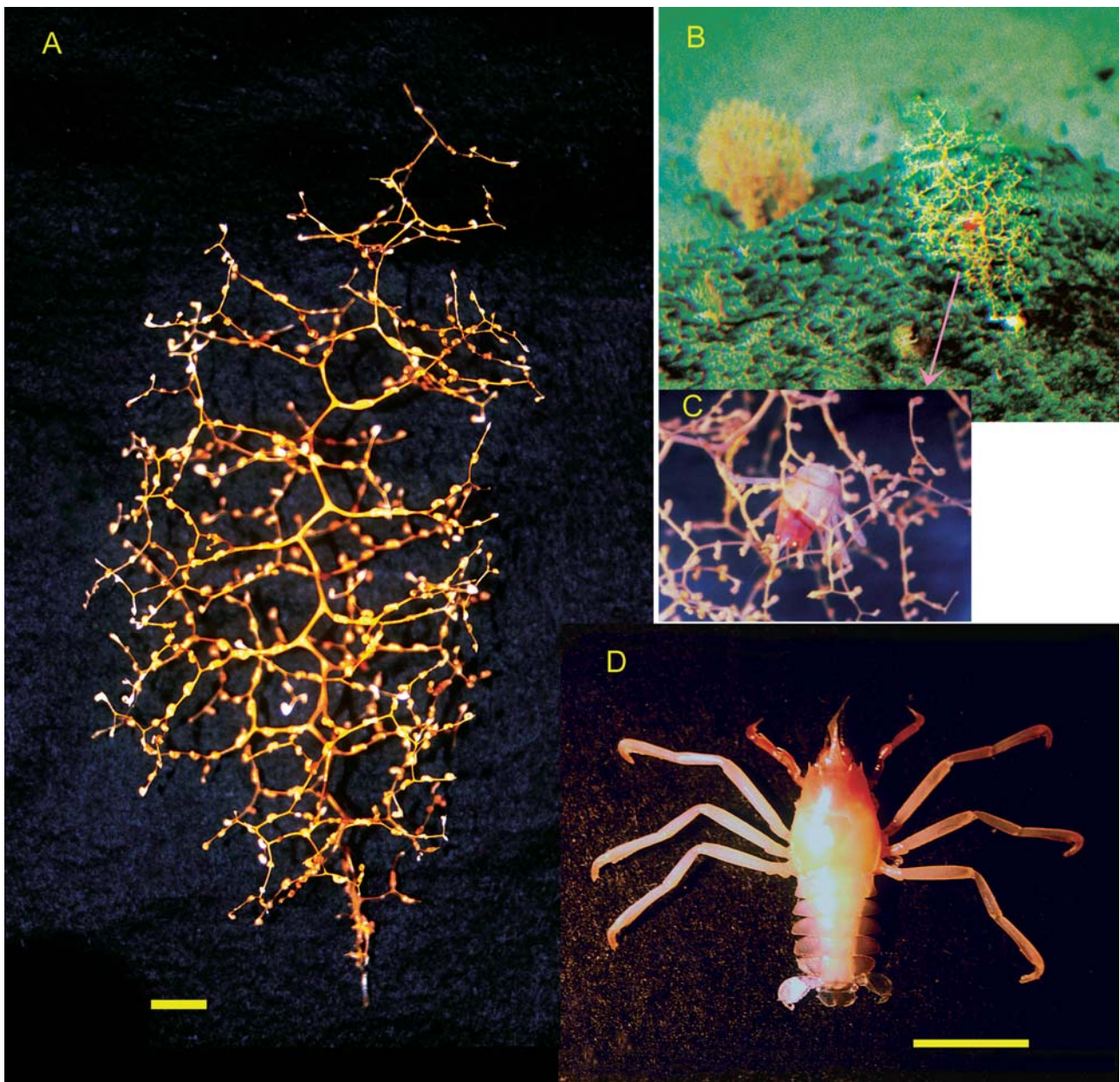


Fig. 4 The 'Christmas Tree' octocorallian (a) as specimen and (b) in situ, attached to a rock surface at 1342 m depth. In (b), note the presence of a galatheid in the middle of the 'tree'; (c) Collected specimen remaining in the same position. (d) Octocorallian-inhabiting galatheid (note four spines on the posterior margin of carapace; carapace is otherwise smooth without spines on other margins). Scale bars = 1cm.

also interesting to note the presence of two galatheid crabs on this island habitat, one hiding beneath a large actinian (Fig. 5a), suggesting that, though free-living (i.e., type 3), these animals intimately depend upon the presence of large suspension feeders. Figs. 5b and c show another examples of gorgonians using a rock surface (ca. 60 cm across) as anchor point in the middle of sandy substrates.

While rock surfaces are conspicuously used by relatively large-sized gorgonians and other sessile animals, small-bodied taxa also occur, often on surfaces which are less likely to be affected by sand (i.e., higher surfaces): Fig. 5d-f show small octocorallians and a cirriped crustacean occurring on surfaces some distance away from sandy substrates (type 1).

Finally, deep-sea crinoids as mobile suspension feeders (i.e., type 3) were also common in the sandy fields. Although physically mobile, these animals were always observed being attached to hard surfaces with little or no (arm) movement (Fig. 5b: *Pentametrocrinus tuberculatus* and probably *Comatulides decameros* (A.H. Clark); Fig. 6a: *P. tuberculatus*; Fig. 6b: probably *Parametra orion* (A.H. Clark)). It is notable that *C. decameros* (Fig. 5b) was attached to a gorgonian on a rock, apparently taking a posture in which the animal was well exposed to the current; in shallow waters crinoids are often observed being attached to scleractinian corals and large sponges on reef edges and walls where the currents are relatively strong. Other mobile organisms including caridean shrimps (e.g. Fig. 6c) were also observed on rock surfaces in the sandy fields.

4. Concluding remarks

Clearly, suspension-feeding anthozoans, particularly octocorallians such as gorgonians, were the most dominant faunal component in the sandy fields of the An'ei Seamount. It is also notable that other taxa such as ophiuroids and galatheid crabs were closely associated with the biogenic habitats provided by the anthozoans.

The procurement of a suitable attachment site is a crucial aspect in the lives of macroinvertebrates inhabiting sandy fields, particularly suspension feeders which rely on current-borne particles as food resources. While this issue is common to animals living at any depth, the problem is more acute for deep-sea organisms as organic particle density is much reduced in deeper waters.

This would necessitate, for example, access to a higher layer of water where currents are faster and more constant, which in turn means that particle supply rate is higher. The acquisition of an elongated stem in gorgonians and stalked crinoids must have been linked to the advantage of placing particle-capturing organs (polyps, tentacles) at a higher position (i.e., above the benthic boundary layer). Further, the fact that some invertebrates use those relatively tall organisms as attachment site also suggests that they are exploiting such vantage habitats for suspension feeding, even at the cost of acquiring morphological change (e.g. elongated arms of ophiuroids associated with gorgonians). Indeed, commensal life on sessile animals under these circumstances makes a switch to free-living very difficult, and therefore a road to closer, obligate commensalism is open.

As sandy fields occur extensively in deep-sea environments, an ability to disperse and utilise rocky, small 'island' habitats in sandy 'seas' is a clear evolutionary advantage to these deep-sea organisms. In this respect, living in a sandy field may be considered not as a 'default' option for these essentially hard-bottom invertebrates, but a significant step that could contribute to the evolutionary persistence and spread of the species. This also raises questions about the mechanisms that allow species coexistence among these taxa (see Tokeshi (1999) for a general review), as different species were often observed together in small, isolated space (hard surfaces). Further research on deep-sea sandy fields may therefore provide data that could make a significant contribution to the general advancement of evolutionary and community ecology.

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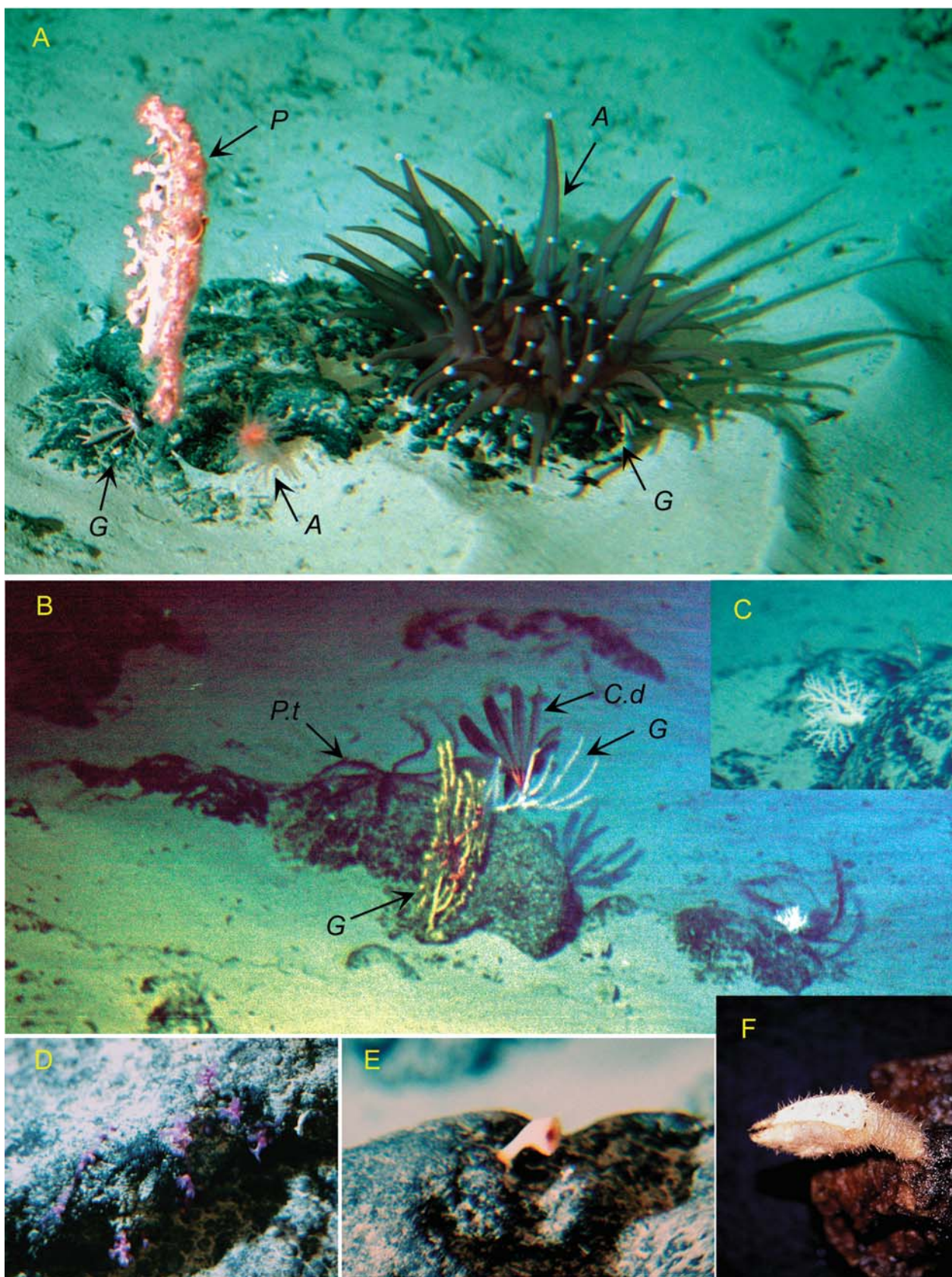


Fig. 5 (a) Rock island inhabited by different macroinvertebrate taxa at 1342 m depth. Two actinians (indicated by A), one pennatulacean (P), and two galatheids (G) are visible. The pennatulacean also harbours an unidentifiable organism on its body. (b) Rock island inhabited by gorgonians (G, yellow and white) and two species of crinoids (*P.t* and *C.d*) at 1342 m depth. The yellow gorgonian harbours (probably) an ophiuroid, while a crinoid (probably *Comatulides decameros*) is perched on the white gorgonian. (c) A gorgonian attached to a rock. (d) Small octocorallians (purple). (e) Unidentified octocorallian. (f) A cirriped crustacean.

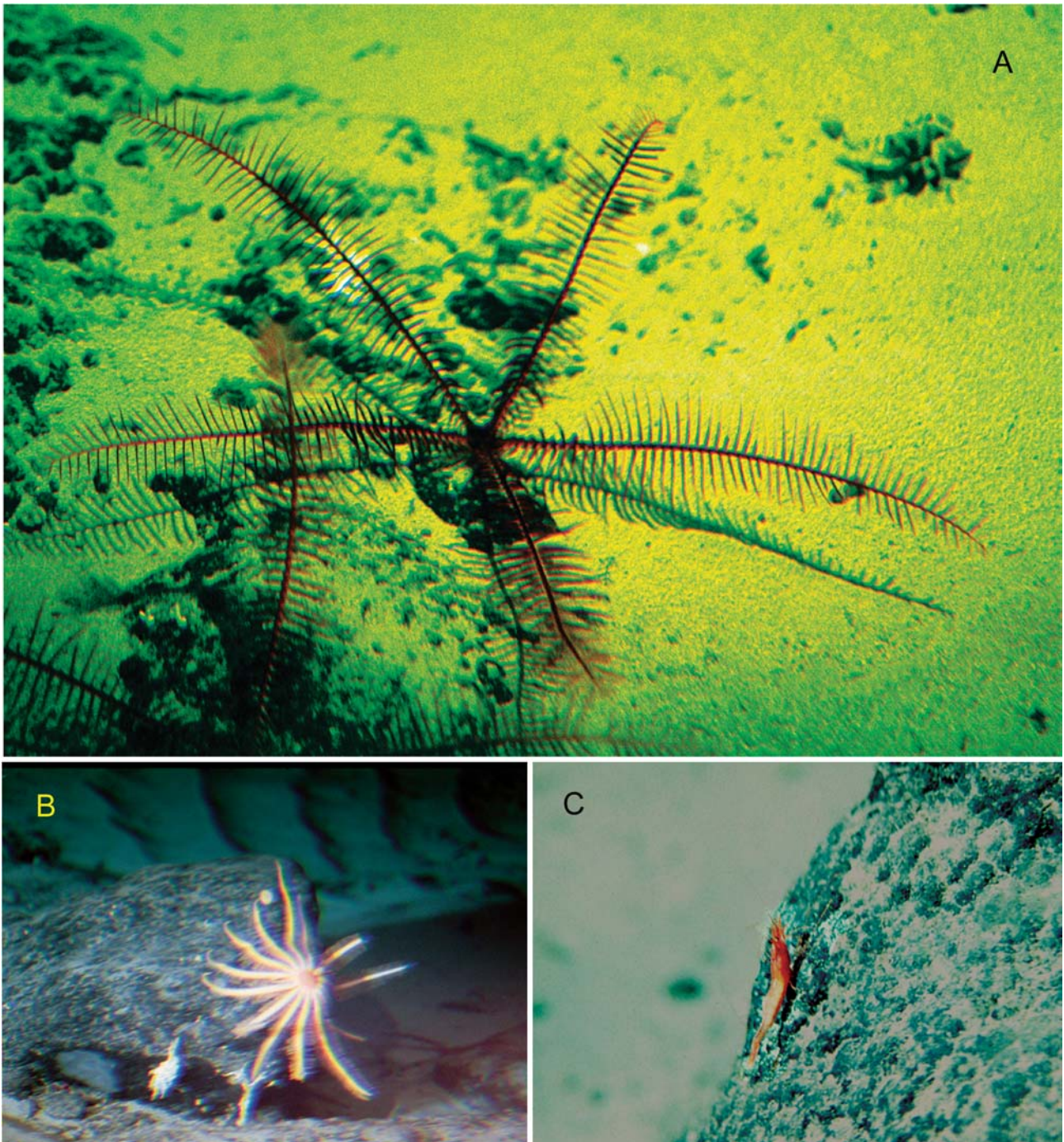


Fig. 6 Mobile fauna perched on rock surfaces in sandy fields. (a) *Pentametrocrinus tuberculatus*, at 1477 m. (b) A crinoid, probably *Parametra orion*, at 1343 m. (c) Unidentified caridean shrimp at 1342 m.

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