

Assessing feeding electivity in *Acanthaster planci*: a null model analysis

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Abstract Feeding electivity was investigated in a non-outbreaking population of the crown-of-thorns starfish *Acanthaster planci* (L.) from North Sulawesi, Indonesia. A null model-based approach was used to assess the feeding pattern of *Acanthaster* in relation to the availability of coral prey in the field. Of a total of 70 species of corals recorded as prey, massive species, particularly of Faviidae, tended to be more frequently consumed than would be expected under the assumption of random feeding by *A. planci*. Branched and encrusting/laminar forms of corals that occurred in relatively exposed sites were apparently not preferred, pointing to the importance of non-acroporan massive species of corals in cryptic habitats as prey for *A. planci*. The null model-based electivity index Z introduced here directly measured the deviation from random feeding, while two common indices (Ivlev's and Vanderploeg and Scavia's) only partially reflected such deviations (hence, prey selection cannot be accurately demonstrated by these). Electivity values (Z) for poritid species and *Acropora palifera*, the most common *Acropora* species in the study site, were significantly negative, indicating apparent avoidance of them by *Acanthaster*. Our results indicate that accessibility to different coral species and the choice/avoidance of certain species are the important elements of feeding in non-outbreaking populations of *Acanthaster* inhabiting spatially variable reef environments. A similar consideration may apply to the feeding patterns of other corallivores that possess superior/inferior mobility to

Acanthaster. The present study emphasizes the merit of testing the observed patterns, using null models for a rigorous assessment of feeding preferences.

Keywords Electivity index · Crown-of-thorns starfish · Faviidae · Prey selection · Corallivore · Sulawesi

Introduction

Among many organisms associated with coral reefs, the crown-of-thorns starfish *Acanthaster planci* (L.) is one of the most important predators of corals with its wide distribution in the Indo-Pacific and destructive effects upon coral reefs. A large body of information has been accumulated on its general biology and ecology (Moran 1986; Birkeland and Lucas 1990), including the aspects of predation. Particular attention has been drawn to its ability to feed on scleractinian corals and to cause massive mortality among them; a widely held view is that the species preferentially feeds on tabular and branched corals of the genus *Acropora* (Keesing and Lucas 1992; De'ath and Moran 1998; Pratchett 2007). On the other hand, while much attention has been drawn to its population outbreaks and consequent, often dramatic, decimation of coral reefs (Done 1985; Yamaguchi 1986; Birkeland and Lucas 1990; Berumen and Pratchett 2006; Pratchett 2005a; Pratchett et al. 2009; Kenyon and Aeby 2009), there is remarkably little detailed information on its predatory habit in different reef sites during the periods in which the species occurs at relatively low- to intermediate-densities. It has been suggested that the starfish's feeding behavior may change with their densities, with food selectivity being high at low densities and declining with increasing densities and scarcity of corals toward the end of an outbreak (Birkeland and

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Lucas 1990). For a comprehensive understanding of the ecology of this important predator, more information is needed on its feeding patterns, particularly under non-outbreak conditions.

One of the difficulties in deciphering the feeding patterns of versatile predators such as *Acanthaster* in open habitats concerns the assessment of preferential/non-preferential feeding. Even if laboratory/controlled field experiments indicate a possibility of selective feeding on some prey categories, data from natural field conditions cannot readily be interpreted as showing the occurrence of preferential/non-preferential feeding, unless the observed patterns are demonstrably different from patterns expected by chance. In the case of *Acanthaster* feeding, however, there has been no study to date that has rigorously tested the departures of field-observed data from random or by-chance patterns. Further, while electivity indices have sometimes been used to interpret data on feeding patterns, the relationship between index values and the degree of deviation from randomness has rarely been checked or clarified. It is, therefore, important to recognize that different electivity indices may vary in their indications of feeding preference and avoidance patterns.

The present study employs a null model approach for explicitly assessing deviations from random patterns of feeding, while taking into account the availability of different prey, in order to elucidate the feeding patterns of *Acanthaster* under non-outbreak conditions. While null model-based analyses have been adopted in a variety of studies on community structure and interspecific patterns (Gotelli and Graves 1996; Tokeshi 1999; Arakaki and Tokeshi 2010), there is a paucity of such analyses on the feeding ecology of marine predators.

Materials and methods

Data collection

Data on the feeding of *Acanthaster* were collected on the eastern side of Bunaken Island (124°47'E, 1°37'N) in North Sulawesi, eastern Indonesia, in 2006–2008. According to our continuous observation of coral assemblages since 2000, the occurrence of *A. plani* on the eastern reefs of Bunaken Island has been low to intermediate with no evidence of past outbreaks or reef devastation (*Acanthaster* density of 0.7–6.5 individuals ha⁻¹ in 2005–2009, which is well below the suggested threshold levels of outbreaking *Acanthaster* populations on the Great Barrier Reef; e.g., ≥ 15 individuals ha⁻¹, Moran and De'ath 1992; >10 ha⁻¹, Keesing and Lucas 1992). In contrast, on partially enclosed reefs of the southern side of the island, which have been heavily exploited by both subsistence

fisheries and the local diving industry, there have been heavy concentrations of *A. plani* since 2003 (>20 individuals ha⁻¹ in 2006–2009) that have caused extensive reef damages, alongside anthropogenic influences (due to people using reefs in various manners; fishing, shellfish collection, trampling, abrasion by snorkelers, etc.). The outbreaking populations of *Acanthaster* gradually moved from east to west within the southern reefs of Bunaken, and coral devastation was widespread in the south-central reef flats by November 2009; however, the reefs on the eastern coast of the island, with distinct topography and reef morphology, were free from *Acanthaster* outbreaks until the end of 2009.

Feeding habits of *A. plani* were observed in the shallow reef habitats (about 4 km long by 80–150 m wide) on the eastern side of Bunaken Island, where reef flats gradually gave way to reef slopes offshore without forming apparent reef edges or crests. Shallow reefs between about 1–7 m of depth, where scleractinian corals were most abundant, were systematically searched using SCUBA, taking note of the occurrence of corals with feeding scars (dead patches of coral, 0.2–0.5 m in longest dimension) and *Acanthaster* individuals in contiguous quadrats (10 by 5 m). In areas with low density of feeding scars and *Acanthaster*, 50 by 10 m quadrats were also employed, depending on the local topography. *A. plani* individuals we observed in our study site were all similar in size (in the range of 20–30 cm diameter) and hence believed to be of the same cohort. The relative abundances of coral species were separately assessed using a total of 27 transects, each 10-m long, noting the shapes and sizes of colonies traversed by a transect line.

For comparing coral growth forms, we have adopted a simple system of classification with 5 forms only: massive, encrusting, laminar, branched, and tabular. While many corals change forms as they grow and in different microhabitats, we designated a most representative form observed for each coral species in the state they were consumed by *A. plani*. Growth forms of 'free-living' fungiid species were categorized as 'laminar', because their exposed body surfaces were roughly in one plane.

Null models and a new electivity index

Feeding data were analyzed by comparing the observed frequencies of feeding on different coral species with values derived from null models in which starfishes were assumed to forage randomly on available corals. For calculating the expected frequencies of feeding under the assumption of no positive/negative feeding choices, corals consumed were selected randomly among all species depending on the availability of each species for the same number of feeding incidences (feeding scars) as observed,

and the process was replicated 10,000 times. The availability of different coral species was expressed as proportional abundance values in two different ways: model 1 used total estimated cover (area) of colonies, while model 2 used total perimeter lengths. Thus, these models assumed that *Acanthaster*'s choice of coral prey was dependent upon their relative abundances expressed as either one- or two-dimensional measures of colony size. This analysis was conducted separately for two different taxonomic resolutions: the genera-based classification and the species-based classification of coral prey. Using these models, electivity (Z) of a particular coral species or genus by *Acanthaster* was calculated as

$$Z = g_0 - g_1$$

where g_0 (g_1) is the proportion of simulations with the calculated values of feeding frequency smaller (larger) than the observed value ($0 \leq g_0, g_1 \leq 1.0$ and $0 \leq g_0 + g_1 \leq 1.0$). Z ranges from 1.0, the maximum (positive) electivity, to -1.0 , the minimum (negative) electivity, while values around zero indicate random feeding based on availability. This index has an advantage of showing the tendencies of preference and avoidance as positive and negative values and enables the comparisons of unconsumed potential prey alongside the assessment of those prey actually consumed. Another advantage is that index values can closely reflect their statistical significance. The positive/negative electivity values were judged to be significant (i.e., significant preference or avoidance of a particular species), if $\max(g_0, g_1) > 0.975$, corresponding to $P < 0.05$ in a two-tailed test ($\max(g_0, g_1) > 0.995$ for $P < 0.01$ and $\max(g_0, g_1) > 0.9995$ for $P < 0.001$).

The performance of this index was compared with two other indices of electivity, Ivlev's (1961) (E_i) and Vanderploeg and Scavia's (1979) (W_i), using the same feeding data. The indices are

$$E_i = (r_i - p_i)/(r_i + p_i)$$

$$W_i = (X - n^{-1})/(X + n^{-1})$$

$$\text{where } X = (r_i/p_i)/\sum(r_i/p_i)$$

where r_i and p_i are the proportions of prey/food i in the diet and in the environment, respectively, and n is the number of kinds of food. Another index by Jacobs (1974), $D_i = (r_i - p_i)/(r_i + p_i - 2r_i p_i)$, was also tested, but its values were very close to Ivlev's (as expected from its formulation) and, therefore, not included in the results. While these indices are supposed to give a quantitative measure of deviation from random feeding, no formal examination of such deviation has been conducted. These indices were each plotted against Z to see how well the latter's data structure (i.e., degree of departure from randomness) is reflected in E or W .

Results

Feeding electivity in *Acanthaster*

A total of 46 coral genera recorded from the study site on the east coast of Bunaken divided into two equal-numbered groups in terms of feeding preferences by *Acanthaster*, one with positive values of electivity (Z) and the other with negative values (Fig. 1). Genera of the family Faviidae dominated the group with positive Z values, with *Favites*, *Goniastrea*, and *Montastrea* showing the three highest electivity values and seven out of ten highest ranking

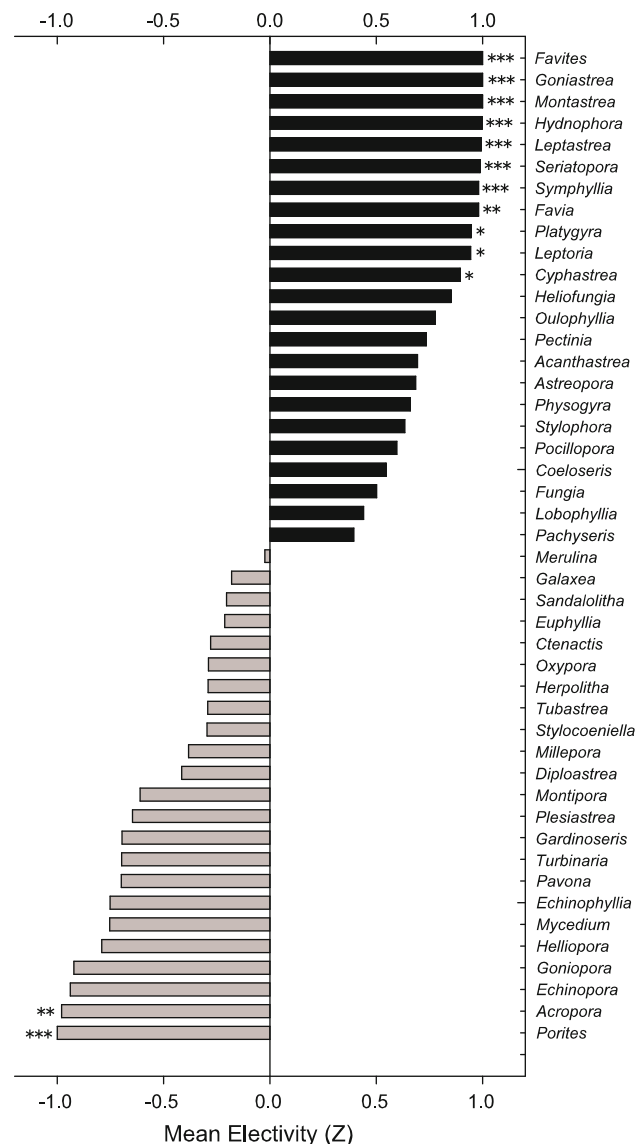


Fig. 1 Electivity (Z) values of different coral genera as prey by *Acanthaster planci* in the shallow reef habitats on the east coast of Bunaken, North Sulawesi. The mean of Z values derived from models 1 and 2 is given for each genus. A significant departure from randomness is indicated by *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

genera belonging to this family. In contrast, the group with negative Z values included diverse genera belonging to different families, with *Acropora* and *Porites* showing strongly negative electivity values. Of those genera with relatively weak electivity values ($-0.5 < Z < 0.5$), negative values occurred more frequently than positive ones, indicating a fairly sharp discrepancy between preferred and non-preferred prey groups.

From a total of 154 feeding scars observed, 70 species of corals were identified as being consumed by *Acanthaster* (Table 1). Electivity values were variable among different coral species, ranging from 1 to -1 , but the majority of species (61 spp.) yielded positive values with only nine species demonstrating negative ones. The values from two null models were highly correlated ($P < 0.001$) and yielded similar results. Of all species, 18 species had positive Z values that were judged to be significantly large on the basis of model 1, of which 11 species belonged to Faviidae. While species of Faviidae showed predominantly positive electivity values, Acroporidae showed a mixed pattern with both positive and negative electivity values among different species. Of nine species that showed negative electivity, values for *Acropora palifera* and *Porites cylindrica* were significant ($P < 0.01$ and $P < 0.001$, respectively) on the basis of model 1, indicating a clear tendency of avoidance of these species by *Acanthaster*.

In terms of coral morphology, massive forms were more predominant (34 spp.; Table 1, Fig. 2) than branched ones (18 spp.) among consumed corals, while encrusting and laminar forms were also frequently consumed (18 spp.). Among massive corals, *Goniastrea* spp. and *Favites abdita* were common and preferred prey ($Z \approx 1$, $P < 0.01$), and species with large polyps such as *Symphyllia* and *Oulophyllia* (Fig. 2e, f) were also consumed. Other common prey were encrusting/laminar forms of *Montipora*, including *M. danae* and *M. grisea*. It was also notable that a species of *Millepora*, non-scleractinian corals generally reported to be free from *Acanthaster* predation (Endean 1973; Glynn 1973; Lewis 1989, but see Keesing 1992), was observed to fall prey (Fig. 2d). Among branched forms, *Hydnophora rigida* and *Seriatopora hystrix* were frequently consumed (Fig. 2h), with significantly high levels of feeding preference ($Z \approx 1$, $P < 0.01$).

Performance of electivity indices

Plotting of Ivlev's E and Vanderploeg and Scavia's W against Z (Fig. 3) shows that E and W indices do not necessarily reflect deviation from random feeding. For relatively large deviation from randomness (e.g., $Z > 0.8$), both E and W tend to show increasing scatter (variation along y axis), indicating that the degree of deviation is not

Table 1 List of coral species preyed upon by *Acanthaster planci* in east Bunaken, North Sulawesi, Indonesia

Species	Form	Electivity Z	
		Model1	Model2
Faviidae			
<i>Goniastrea minuta</i>	<i>m</i>	0.9999***	0.9974**
<i>Goniastrea edwardsi</i>	<i>m</i>	0.9831*	0.9981**
<i>Favia matthaii</i>	<i>m</i>	0.8289	0.7863
<i>Favia lizardensis</i>	<i>m</i>	0.8739	0.8098
<i>Favia pallida</i>	<i>m</i>	0.9827*	0.8731
<i>Favia veroni</i>	<i>m</i>	0.821	0.4839
<i>Favia stelligera</i>	<i>m</i>	0.8132	0.8698
<i>Favia helianthoides</i>	<i>m</i>	0.1134	-0.0506
<i>Favites spinosa</i>	<i>m</i>	0.9466	0.7328
<i>Favites halicora</i>	<i>m</i>	0.9987**	0.9986**
<i>Favites flexuosa</i>	<i>m</i>	0.9276	0.7604
<i>Favites stylifera</i>	<i>m</i>	0.9946*	0.9257
<i>Favites abdita</i>	<i>m</i>	1.0***	1.0***
<i>Leptastrea bottae</i>	<i>m</i>	1.0***	1.0***
<i>Oulophyllia bennetae</i>	<i>m</i>	0.9071	0.6254
<i>Oulophyllia crispa</i>	<i>m</i>	0.6037	0.4806
<i>Platygyra pini</i>	<i>m</i>	0.9448	0.7863
<i>Platygyra ryukyuensis</i>	<i>m</i>	0.8631	0.6826
<i>Platygyra sinensis</i>	<i>m</i>	0.3603	0.5771
<i>Platygyra verweyi</i>	<i>m</i>	0.8858	0.7138
<i>Leptoria phrygia</i>	<i>m</i>	0.9961**	0.9641
<i>Montastrea colemani</i>	<i>m</i>	0.9999***	0.9969**
<i>Montastrea valenciennesi</i>	<i>m</i>	0.9999***	0.9951**
<i>Cyphastrea ocellina</i>	<i>m</i>	0.9913*	0.9073
<i>Cyphastrea agassizi</i>	<i>m</i>	0.8244	0.4858
Mussidae			
<i>Acanthastrea faviaformis</i>	<i>m</i>	0.9645	0.7681
<i>Lobophyllia hemprichii</i>	<i>m</i>	0.2783	0.535
<i>Symphyllia recta</i>	<i>m</i>	1.0***	0.9977**
Agariciidae			
<i>Coeloseris mayerii</i>	<i>m</i>	0.5818	0.4623
<i>Pachiseris gemmae</i>	<i>l</i>	0.9891*	0.9345
Euphyllidae			
<i>Physogyra lichtensteini</i>	<i>m</i>	0.8184	0.495
Oculinidae			
<i>Galaxea astreata</i>	<i>m</i>	0.8601	0.5471
Pectiniidae			
<i>Echinopora lamellosa</i>	<i>l</i>	-0.8806	-0.6135
<i>Pectinia paeonia</i>	<i>l</i>	0.2654	0.024
<i>Pectinia lactuca</i>	<i>l</i>	0.9351	0.7653
Acroporidae			
<i>Montipora confusa</i>	<i>e</i>	0.9114	0.6346
<i>Montipora danae</i>	<i>e</i>	0.9978**	0.9506
<i>Montipora efflorescens</i>	<i>e</i>	0.6922	0.529
<i>Montipora grisea</i>	<i>e</i>	0.9972**	0.9691

Table 1 continued

Species	Form	Electivity Z	
		Model1	Model2
<i>Montipora informis</i>	<i>e</i>	0.707	0.3587
<i>Montipora foliosa</i>	<i>l</i>	0.9524	0.7235
<i>Montipora porites</i>	<i>b</i>	0.9545	0.7254
<i>Montipora hispida</i>	<i>e</i>	−0.1716	−0.2082
<i>Montipora turtlensis</i>	<i>m/e</i>	0.7293	0.3737
<i>Acropora yongei</i>	<i>b</i>	−0.8448	−0.5807
<i>Acropora solitaryensis</i>	<i>b/t</i>	0.76	0.4069
<i>Acropora brueggemanni</i>	<i>b</i>	0.9149	0.7495
<i>Acropora latistella</i>	<i>b</i>	0.0856	0.2175
<i>Acropora cytherea</i>	<i>b</i>	0.6949	0.5557
<i>Acropora palifera</i>	<i>b</i>	−0.9977**	−0.8528
<i>Acropora kimbeensis</i>	<i>b</i>	0.7045	0.5564
<i>Acropora formosa</i>	<i>b</i>	−0.5373	−0.3869
<i>Astreopora myriophthalma</i>	<i>m</i>	0.8393	0.5221
Pocilloporidae			
<i>Pocillopora damicornis</i>	<i>b</i>	0.9656	0.8331
<i>Pocillopora meandrina</i>	<i>b</i>	0.1732	−0.0332
<i>Pocillopora eydouxi</i>	<i>b</i>	0.5549	0.2412
<i>Pocillopora verrucosa</i>	<i>b</i>	−0.0947	−0.1776
<i>Stylophora pistillata</i>	<i>b</i>	0.5609	0.6635
<i>Seriatopora hystrix</i>	<i>b</i>	1.0***	0.9998***
Poritidae			
<i>Porites cylindrica</i>	<i>b</i>	−1.0***	−0.9446
<i>Alveopora marionensis</i>	<i>m</i>	0.9548	0.7428
Merulinidae			
<i>Merulina scabricula</i>	<i>l</i>	−0.35	0.0233
<i>Merulina ampliata</i>	<i>l</i>	0.4151	0.1228
<i>Hydnophora grandis</i>	<i>b</i>	0.532	0.2143
<i>Hydnophora rigida</i>	<i>b</i>	0.9992**	0.9986**
<i>Hydnophora microconus</i>	<i>m</i>	0.9978**	0.977*
Fungiidae			
<i>Cycloseris erosa</i>	<i>l</i>	0.9502	0.7373
<i>Fungia danai</i>	<i>l</i>	0.9719	0.8499
<i>Heliopora actiniformis</i>	<i>l</i>	0.9552	0.7328
Milleporidae			
<i>Millepora</i> sp.	<i>b</i>	−0.4631	−0.3514

Growth forms are indicated as: *m* massive, *e* encrusting, *l* laminar, *b* branched, *t* tabular. Electivity (*Z*) values based on two null models are shown (* <0.05, ** <0.01, *** <0.001)

accurately expressed by these values. In the case of coral species with significantly large departures of positive *Z* values, corresponding values of *E* varied from 0.470 to 0.977 and *W* from −0.198 to 0.908. On the other hand, both indices correlated well with *Z* under situations not significantly departing from randomness (within an intermediate range of *Z*, $-0.5 < Z < 0.5$). The plot clearly shows that

the minimal values (−1) of these indices do not indicate departures from random feeding.

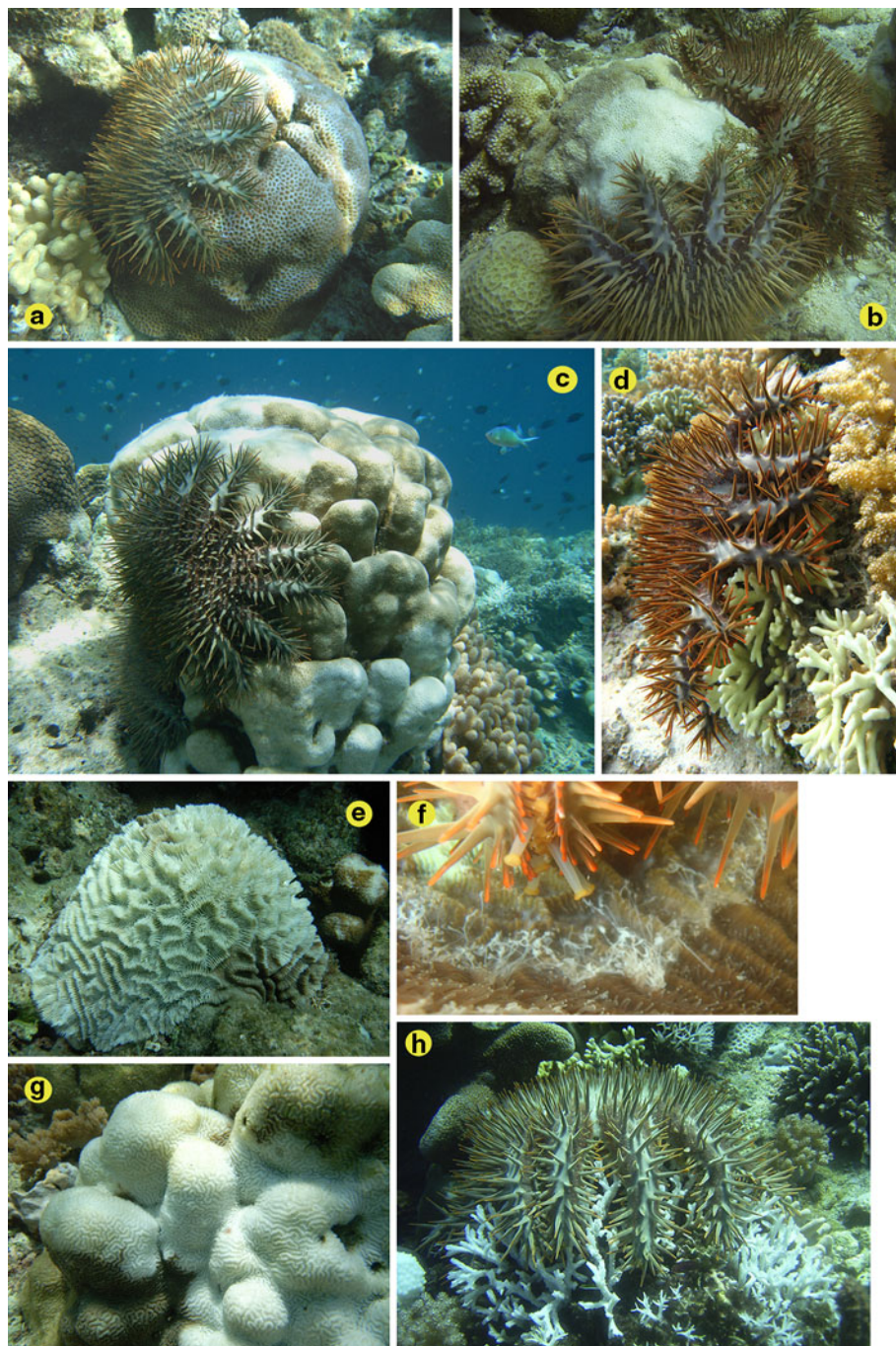
Discussion

Evaluation of feeding electivity

The present study points to the importance of massive corals, particularly the species of Faviidae, as food for a non-outbreaking population of *A. planci* in North Sulawesi. The data clearly demonstrated that faviid species tended to be more preferred by *A. planci* predators than the species of other families. In particular, *Z* values for faviids were significantly higher than those for acroporid species (Mann–Whitney *U* test, $P < 0.001$). At the same time, the study emphasizes the importance of rigorously assessing the preferential/non-preferential feeding of different coral taxa by *A. planci*. In this context, it is worth noting that the widely recognized consumption of tabular and branched *Acropora* species by *A. planci* is not necessarily a fixed or universal behavioral pattern under different reef conditions.

In order to evaluate the feeding tendencies of *A. planci*, the present study adopted an index of electivity that measured the degree of departure from a presumed random mode of feeding. This is based on the idea that an observed pattern of feeding needs to be assessed against the background of non-selective feeding, and this can only be accomplished through simulation of random feeding processes. Just as feeding of a particular prey item may be due either to a chance encounter or to preferential foraging, no consumption of a particular prey category may also be due to either chance or active avoidance. Thus, it is desirable that an index of electivity reflects the degree to which an observed situation departs from a random situation. While this is considered important for a rigorous evaluation of non-random patterns of feeding, no study has examined the performance of conventional indices of electivity in terms of deviations from randomness. The analysis in the present study suggests that use of two common indices of electivity is problematic as their values only partially mirror the degree of deviation from random feeding. The problem is most acute for the assessment of significant feeding preferences, as the values from both Ivlev's index *E* and Vanderploeg and Scavia's *W* are quite variable for relatively high values of *Z* (>0.8). In other words, both of these indices tend to underestimate the cases of significant preferences; for example, feeding on Faviidae species cannot reliably be assessed by these. At the same time, these indices tend to indicate incorrectly negative food selection where in fact there is no significant departure from randomness. Indeed, an example of somewhat complex results of prey selection in corallivorous gastropods

Fig. 2 *Acanthaster planci* feeding on different species of non-acroporan corals in Bunaken, eastern Indonesia. **a** *Goniastrea edwardsi*, note also untouched *Acropora palifera* in the right front; **b** *Leptastrea bottae*; **c** *Favia stelligera*; **d** *Millepora* sp.; **e** *Oulophyllia crispera*; **f** Details of *Oulophyllia crispera* with mesenterial filaments extended to resist in vain the attack of *A. planci*; **g** *Leptoria phrygia*; **h** *Hydnophora rigida* (consumed *Seriatopora hystrix* also visible in the foreground and background; note also untouched *Acropora palifera* in the left back)



(Morton and Blackmore 2009) may be partly due to the use of Jacobs's index (a slight modification of E , see Materials and Methods).

In evaluating feeding electivity, as the encounter rate would vary with the availability of different prey under random feeding, some assumptions must be made regarding prey encounter. However, in the absence of precise information on how *A. planci* detects prey in natural reef environments, some uncertainties always remain as to which characteristics of coral colonies would most strongly

affect their availability to *A. planci* predators. In this regard, given the complex three-dimensional structures of reef environment, the two-dimensional measure of colony size (model 1) is probably more relevant than the one-dimensional measure (model 2), though largely similar results were obtained by both measures.

An analysis of feeding patterns of *A. planci* from the Great Barrier Reef (De'ath and Moran 1998) revealed that species of *Acropora* were most preferred, followed by those of *Montipora*, while massive corals particularly of

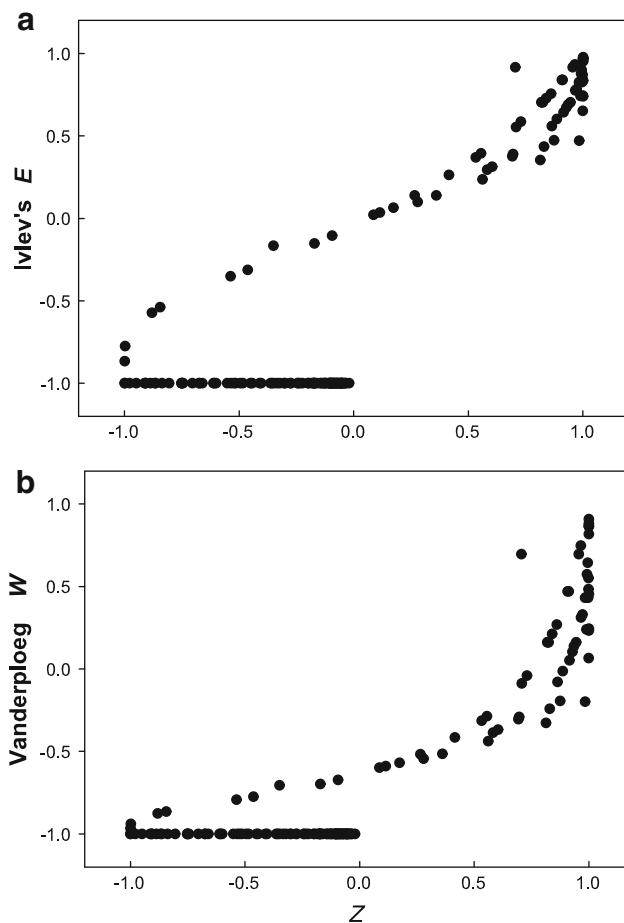


Fig. 3 Relationship between electivity index Z and **a** Ivlev's index E and **b** Vanderploeg and Scavia's index W

the genus *Porites* were not favored. Our result also confirms that massive species of *Porites* such as *P. lobata* and *P. lutea*, which were very common in the study site ($\sim 65\%$ occurrence in all quadrats), were not consumed. It is also worth noting that branched species of *Porites* such as *P. nigrescens* and *P. attenuata* were not preyed upon by *Acanthaster* despite their commonness (combined occurrence $\sim 53\%$); the most abundant of branched *Porites*, *P. cylindrica*, showed the minimal value of Z ($=-1.0$). Therefore, irrespective of growth forms, poritid species in eastern Bunaken are generally not prone to consumption by *Acanthaster*. While some studies reported *Acanthaster* feeding on *Porites* (Goreau 1964; Barnes et al. 1970; Glynn 1974; Done 1985), we rarely found such feeding. Several traits of *Porites* may explain low preference by *Acanthaster* in our study; these include low energetic values, release of repellent substances (Brauer et al. 1970) and the presence of symbiont species that deter the attack by sea-stars (DeVantier et al. 1986; DeVantier and Endean 1988; Pratchett 2001). Another interesting case concerns *Acropora palifera*, a species with stout branches, that had a

particularly low value of Z ($=-0.9977$) despite being the most common species of *Acropora* in the shallow reef habitats (Fig. 2a, h), suggesting that *Acropora* species are not uniformly preferred by the starfish.

Variable feeding in *Acanthaster* and other corallivores

While factors such as 'innate' preferences and previous feeding experiences either as juvenile or as adult may influence prey selection (Collins 1975; Ormond et al. 1976; Pratchett 2007), accessibility to particular coral colonies must also constitute an important, sometimes overriding, factor. In our study site, acroporids in exposed, fast-current habitats and table-formed species standing on a thin central stalk may be far less accessible prey than massive corals of various sizes in a close vicinity of a starfish's refugia. There are also possible deterrence effects of coral symbionts such as toxic gobies and crustaceans that occur in association with different species of *Acropora* (Lassig 1977; Glynn 1980, 1987; Pratchett 2001). Accessibility also appears to be an important factor in the case of solitary fungiid species that are often found in microhabitats not easily accessible for *A. planici*, such as small crevices or among other corals, rubble substrates; indeed, individuals of fungiids in accessible open locations were seen to be readily consumed by the starfish.

The present study has clearly demonstrated that *Acanthaster* in the natural environment is capable of preying upon a diversity of coral species, particularly massive ones. Previous studies on the Great Barrier Reef also drew attention to the predation of massive corals by *A. planici* and their slow recovery after *A. planici* outbreaks (Endean et al. 1989; Cameron et al. 1991). One possibility regarding the starfish's predation behavior is that at low- to intermediate-densities crown-of-thorns individuals may feed on corals that are close to their shelters, most typically the underside of a coral rock. Starfishes are likely to encounter massive and encrusting corals when they crawl out of such hiding places in most shallow reef areas of eastern Bunaken. Feeding on a variety of non-acroporan corals has also been reported for *Acanthaster* populations in the subtropical waters of Okinawa, southern Japan (Keesing 1992).

Apart from *A. planici*, various reef-associated taxa have been known to demonstrate a range of obligate and facultative corallivory and feeding electivity (Cumming 1999; Cole et al. 2008; Rotjan and Lewis 2008). However, except in cases where feeding is apparently restricted to a single or few target species (e.g., a butterflyfish *Chaetodon trifascialis* feeding almost exclusively on *Acropora hyacinthus*, Pratchett 2005b), it is not straightforward to recognize feeding preferences/avoidances in the absence of a null model type test on field-derived data. The present study

draws attention to the importance of assessing the departures of observed feeding patterns from randomly expected patterns. In this regard, as mobility and life-time movements vary among corallivore taxa (fishes, molluscs, etc.), the availability/accessibility of different coral species to a particular corallivore needs to be carefully assessed. For example, while highly mobile corallivorous fishes (e.g., Chaetodontidae) may have access to nearly all coral colonies within a patch of reef, molluscan predators with more restricted mobility (e.g., *Coralliophila*, Hayes 1990; Oren et al. 1998; *Drupella*, Cumming 1999; Morton and Blackmore 2009) may only have limited access to different coral species on relatively small spatial scales. It remains to be seen to what extent different cases of corallivory (e.g., in *Drupella*, Morton and Blackmore 2009) can be recognized as significant departures from random feeding.

Predation patterns in reef environments apparently vary depending on many factors including the local distributions of different coral species. Given the complex variation in species composition and local topography of different reef sites, more research is needed to gain a better understanding of the feeding behavior of corallivores such as *A. planici* under different environmental conditions in a range of spatio-temporal contexts.

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