

A keystone predatory sea star in the intertidal zone is controlled by a higher-order predatory sea star in the subtidal zone

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ABSTRACT: The impact of keystone predators may be affected by physical conditions and interactions with other predators. We evaluated the impact of the sea star *Meyenaster gelatinosus* on another sea star, *Heliaster helianthus*, which was previously described as a keystone predator along the coast of central Chile. Field surveys showed that *H. helianthus* is a common prey of *M. gelatinosus*. *H. helianthus* occurred across the subtidal zone at locations with few *M. gelatinosus*, but was largely restricted to the intertidal and upper-subtidal zones at locations where *M. gelatinosus* was abundant. The proportion of *H. helianthus* feeding decreased with increasing *M. gelatinosus* abundance, and *H. helianthus* with autotomized arms, mainly the result of sublethal attacks by *M. gelatinosus*, increased with increasing *M. gelatinosus* abundance. Additions of *M. gelatinosus* to a sediment bottom area where *H. helianthus* was actively feeding on the gastropod *Turritella cingulata* provoked (1) reduced feeding and (2) a strong escape response in which *H. helianthus* took the 'crown' position (arm tips raised) in about 40 s and then fled. *T. cingulata* is an abundant prey resource that is likely only available to *H. helianthus* when *M. gelatinosus* is rare. The predatory role of *H. helianthus* is greatly reduced when *M. gelatinosus* is common. Our observations suggest that *M. gelatinosus*, rather than *H. helianthus* or the whelk *Concholepas concholepas*, is the keystone predator in subtidal communities. Our study demonstrates that the role of a keystone predator (in our case *H. helianthus* in the intertidal zone) can change in an adjacent habitat (the subtidal zone) due to interactions with other predators.

KEY WORDS: Predator–prey interaction · Sublethal predation · Distribution · Autotomy · Sea star · Ecological role · Keystone · Chile

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INTRODUCTION

Predators strongly affect the ecology of their prey and in turn community structure. Their impact is not limited to reducing prey numbers (Sih et al. 1985), as predators can cause changes in prey morphology (Reimer & Harms-Ringdahl 2001), size (Norberg & Tedengren 1995), spatial distribution (Rochette & Dill 2000, Esser et al. 2004, Yunker 2004), behavior (Lima & Dill 1990, Reimer et al. 1995, Trussell et al. 2003, 2004) and the duration of vulnerable life stages (Dahl & Peckarsky 2003). Predators usually affect the structure

of the communities they inhabit, and keystone predators can control important species that occupy primary space on the sea bottom. This has been illustrated for killer whales in nearshore benthic communities (Estes et al. 1998) and sea star predators in intertidal communities (Paine 1974, Paine et al. 1985, Menge et al. 1994). However, the role of most keystone predators has only been documented for specific habitats. The keystone role of a predator may not extend to all habitats where the predator is found, as its impact may change with physical conditions and interactions with other predators (Power et al. 1996). For example, the

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role of the classic keystone predator *Pisaster ochraceus* in the northeastern North Pacific applies to exposed rocky intertidal habitats, but not to sheltered habitats (Menge et al. 1994).

Paine et al. (1985) reported that the sun star *Heliaster helianthus* is a keystone predator in intertidal communities along the coast of central Chile. Its foraging limits the lower limit of the mussel *Perumytilus purpuratus*, which tends to monopolize rocky surfaces when *H. helianthus* is absent. However, its importance as a predator may change in the subtidal zone. Viviani (1978) suggested that *H. helianthus* is limited to shallow rocky areas because these areas provide it with a refuge from *Meyenaster gelatinosus*, a voracious predatory sea star found from low tide level down to ~25 m in depth. *M. gelatinosus* strongly selects echinoderm prey, such as *H. helianthus* and the black sea urchin *Tetrapygus niger* (Aburto 1999), and provokes strong escape responses from the sea urchin and several species of molluscs (Dayton et al. 1977, Serra et al. 1997, Ortiz et al. 2003, C. F. Gaymer unpubl. data). *H. helianthus* can represent ~15% of the diet of *M. gelatinosus* in northern Chile (Viviani 1978). *M. gelatinosus* likely completely consumes small *H. helianthus*; however, interactions with large *H. helianthus* are usually not lethal, but can result in arm loss (as many as 9 arms in 1 attack; Viviani 1978). Non-lethal effects may cause indirect interactions that may lead to important changes in community structure. Trait-mediated indirect interactions have recently been reviewed for different systems and may drive trophic cascades (Abrams et al. 1996).

Our recent observations of subtidal communities in central and northern Chile show that *Heliaster helianthus* can occur throughout the rocky subtidal zone and suggest that its abundance and distribution is negatively related to the abundance of *Meyenaster gelatinosus*. Such changes in the distribution of *H. helianthus* should in turn affect its predatory role in different habitats. The present study evaluates the impact of *M. gelatinosus* on *H. helianthus*, specifically on its distribution, access to food, feeding activity and its importance as a predator in subtidal communities. We show that the role of a keystone predator in one habitat can be modified by interactions with a higher-order predator in an adjacent habitat.

MATERIALS AND METHODS

Study sites. We quantified the distribution and feeding of *Heliaster helianthus* and *Meyenaster gelatinosus* at 4 locations: Flamenco and Ramada, where both sea star species were common, and Bahía Cisnes and Obispito, where *H. helianthus* was common but

M. gelatinosus was rare. All 4 locations were within a 100 km section of coastline in central–northern Chile (26° 34' 21.6" S to 27° 14' 55" S), were similar in respect to exposure to waves and supported similar potential prey. Also, at all locations the bottom was mainly a gently sloped bedrock platform which extended to about 7 m in depth, where a sediment slope began. At each location there was a narrow belt of the kelp *Lessonia nigrescens* down to 1 m in depth followed by sea urchin barrens, which extended to the end of the rocky zone. The barrens occasionally supported patches of the mussel *Semimytilus algosus*, the tunicate *Pyura chilensis*, the gastropods *Tegula* spp., *Crepidula* spp. and *Calyptrea trochiformis*, and barnacles. The sediment slope supported extremely high densities of the detritivorous gastropod *Turritella cingulata* (up to ~4000 ind. m⁻²).

Field sampling. At each location, we quantified depth, substratum type and prey availability along 5 transects that ran perpendicular to the shore, from the low tide level to several meters into the sediment bottom (ending at 7 to 11 m below lowest water of spring tides [LWST]). The transects were spaced at 20 m intervals along the shore. We examined 1 m² quadrats placed at 1 m intervals, on alternating sides of each transect (the side of the first quadrat was chosen at random), and recorded (1) depth, (2) percentage cover of different substrata (sand, pebbles, cobbles, boulders and bedrock; as defined by Wentworth 1922) and (3) numbers of major prey items. Further, for each quadrat we recorded the number and radius (distance from the center of the disc to the end of the longest arm) of each *Heliaster helianthus* and *Meyenaster gelatinosus*, and noted when *H. helianthus* showed arm autotomy (loss of arms). We also recorded whether each sea star was feeding, and if so, identified and measured the size of the prey. The sampling at Flamenco, Ramada and Bahía Cisnes was done during winter 2003 and 2004, and during summer 2004 and 2005; the sampling at Obispito was done in winter 2003 and summer 2004. The quadrat data permitted us to calculate Yule's *V* selectivity index (Kendall 1947), as an index of prey selection relative to availability (Pearre 1982). The coefficient ranges from -1 to +1, with 0 indicating that prey are consumed according to availability.

As there were no marked differences in the densities of *Heliaster helianthus* and *Meyenaster gelatinosus* on different sampling dates at each study location, values were pooled for each sea star at each location. For each location, we applied a 1-way ANOVA to evaluate whether the size of *H. helianthus* varied with depth and a crossed 2-way ANOVA to test for differences in the density of the 2 sea star species (fixed factor) with depth (fixed factor) (all sampling dates pooled). The quadrats taken within each 2 m depth interval were

used as replicates for these analyses. Data were log-transformed ($\ln(y + 1)$) when necessary to obtain normality and homoscedasticity of the data. Normality was tested using the Shapiro-Wilk test (SAS Institute 1991) and homogeneity of variances using the Levene test (Snedecor & Cochran 1989). When these assumptions were not met, the ANOVAs were applied to both the raw and rank-transformed data, as suggested by Conover (1980). The former was chosen for presentation when results were the same for the 2 analyses and the latter when they were not. A multiple pairwise comparison test (least-square means) was used to test for specific differences within a significant source of variation (SAS Institute 1991). We tested for differences in the proportion of *H. helianthus* feeding, and showing arm autotomy, using a generalized linear model with a binomial distribution and an incomplete factorial design (McCullagh & Nelder 1989) and followed with multiple comparisons using Glimmix's macro (Littell et al. 1996).

To examine whether there was an association between the abundance of *Heliaster helianthus* and that of *Meyenaster gelatinosus*, we applied a correlation analysis to their densities observed in the 641 quadrats sampled over 2.5 yr. We further tested whether (1) the proportion of *H. helianthus* showing arm autotomy and (2) the proportion of *H. helianthus* that were feeding were correlated with the abundance of *M. gelatinosus*, and *t*-tests were used to evaluate whether Spearman rank correlation coefficients (r_s) were significant (Steel & Torrie 1980).

Effect of *Meyenaster gelatinosus* additions on *Heliaster helianthus* in the field. To study responses of *H. helianthus* to *M. gelatinosus*, we ran field experiments in 2004 on the sediment bottom at Bahía Cisnes. At this location *M. gelatinosus* was rare on the rocky bottom and absent on the deeper sediment slope. The experiments were performed in 13 circular areas measuring 3 m in diameter, each delineated by sticks that were driven into the sediment bottom along the circumference of the area. There were naturally ca. 8 *H. helianthus* in each circular area (~ 1.1 ind. m^{-2}), and all were feeding on the gastropod *Turritella cingulata*, which was extremely abundant in this area. Just prior to each trial, we quantified the proportion of *H. helianthus* that were feeding (a humped position is taken when prey are being digested, Fig. 1). We started each trial by adding 4 large *M. gelatinosus* (15 to 18 cm radius) to the center of the circular area, without disturbing the *H. helianthus* naturally present in the area. This resulted in a *M. gelatinosus* density in the circular area equivalent to the maximal abundance observed at Flamenco and Ramada (~ 0.6 ind. m^{-2}). We then recorded the behavior and position of *H. helianthus* over time (at 5 to 10 min intervals), using digital

chronometers and graduated plastic rods, until all *H. helianthus* had left the circular area (the end of the trial). We noted (1) when each *H. helianthus* left the circular area and (2) whether it was feeding as it left (*H. helianthus* can feed as it moves). As moving sea stars lost their humped position, feeding was checked by turning sea stars over to see if the stomach was evaginated over a prey item. Seven trials were conducted in this way, and no *M. gelatinosus* were added to the remaining 6 areas that served as controls. During the course of these trials other sea stars observed near the experimental areas were removed.

We applied a crossed 2-way ANOVA to test for differences between control and *Meyenaster gelatinosus* addition areas (fixed factor) in the proportion of *Heliaster helianthus* that left the circular areas at different times (fixed factor). Data were arcsine-transformed when necessary to obtain normality and homoscedasticity of the data. Normality, homogeneity of variances and multiple comparisons were made as described in the previous section. Differences in percentage feeding were evaluated in the same way as proportion feeding in the transects.

During the above experiment, and on other occasions, we noted that *Heliaster helianthus* displayed a striking escape response when touched by *Meyenaster gelatinosus*. Thus, we ran trials while diving ($n = 43$) to quantify this behavior. In each trial, we placed 1 arm of a large *M. gelatinosus* on top of a feeding *H. helianthus* and then, using a chronometer, recorded the behaviors of the *H. helianthus* until it was no longer in contact with the *M. gelatinosus*. Different sea stars were used in each trial.

RESULTS

Distribution and abundance of sea stars

Heliaster helianthus showed 2 distinct distributional patterns with respect to depth. At Flamenco and Ramada, where *Meyenaster gelatinosus* was common, *H. helianthus* was restricted to the first 4 m in depth. This corresponded to the zone just below the belt of the kelp *Lessonia nigrescens* in the intertidal zone. Densities peaked at ~ 0.7 m^{-2} at 1 m in depth, fell to ~ 0.2 m^{-2} at 3 m and to 0 m^{-2} at > 4 m (Table 1, Fig. 2). The reduction in numbers of *H. helianthus* at 3 m coincided with the zone where the abundance of *M. gelatinosus* peaked (~ 0.5 ind. m^{-2}). In contrast, at Bahía Cisnes and Obispito, where *M. gelatinosus* densities were consistently low (< 0.1 ind. m^{-2}), *H. helianthus* occurred throughout the rocky subtidal zone and also extended well into the sediment bottom zone with densities of 0.7 to 1.3 m^{-2} . Although *M. gelatinosus* densi-

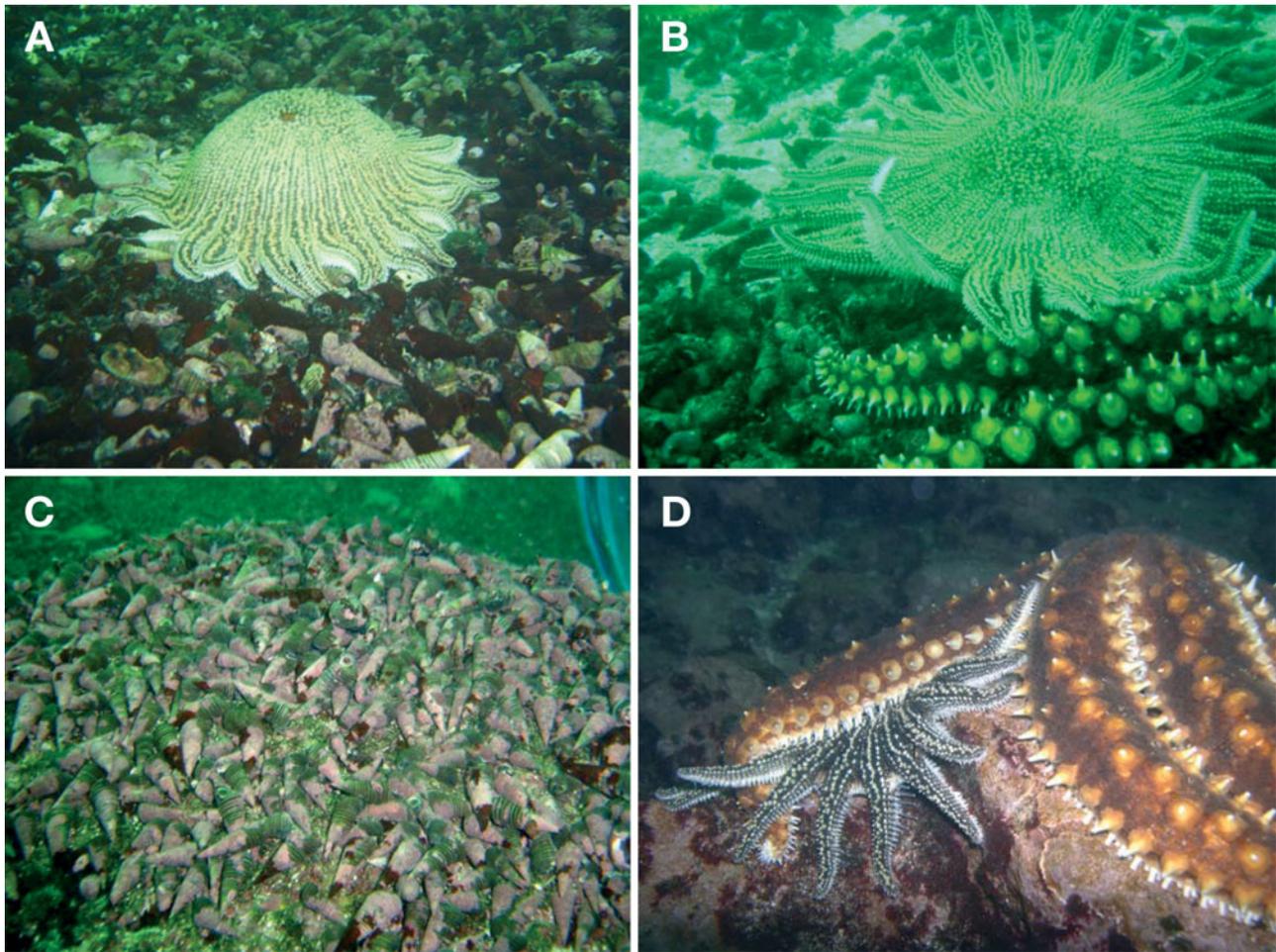


Fig. 1. *Heliaster helianthus*, *Turretella cingulata* and *Meyenaster gelatinosus*. (A) *H. helianthus* in humped position while feeding on the gastropod *T. cingulata*; (B) *H. helianthus* beginning to take on the 'crown' position (arm tips raised) in response to contact with its predator *M. gelatinosus*; (C) *T. cingulata* covering the sediment bottom at Bahía Cisnes; (D) *M. gelatinosus* capturing *H. helianthus* on a rocky slope. Note the large size and thick arms of *M. gelatinosus* in contrast to smaller and thinner body of *H. helianthus*

ties were low throughout the rocky zone at Bahía Cisnes and Obispito, we nevertheless observed decreases in the density of *H. helianthus* at the depths where the density of *M. gelatinosus* showed slight increases (Table 1, Fig. 2). In spite of the overall inverse abundance patterns for the 2 sea stars, the 2 species were not segregated at a small scale (the scale of our 1 m² sampling quadrats) as no correlation was detected between density values for the 2 sea stars in the quadrats taken at any of the 4 locations (Flamenco, $r_S = 0.08$, $p = 0.21$; Ramada, $r_S = -0.02$, $p = 0.78$; Bahía Cisnes, $r_S = 0.06$, $p = 0.42$; Obispito $r_S = 0.02$, $p = 0.87$).

The size of *Heliaster helianthus* at different depths also varied between the locations with high and low abundance of *Meyenaster gelatinosus* (Fig. 3). At Flamenco and Ramada, where *M. gelatinosus* was common, average size increased with depth, because smaller individuals (~ 6 to 8 cm in radius) were

restricted to the intertidal (Flamenco) or upper subtidal (Ramada) zones. In contrast, at Bahía Cisnes, where *M. gelatinosus* was rare, smaller *H. helianthus* were found on soft bottoms at greater depths and larger individuals (~20 cm) at shallower depths. At Obispito, where *M. gelatinosus* was also rare, *H. helianthus* size did not vary significantly with depth ($p = 0.68$), although small individuals tended to be more common at greater depths (Fig. 3).

An additional survey at Flamenco in 2006 showed that the distribution of *Heliaster helianthus* was even more restricted than in the initial surveys in 2004 and 2005, as it had disappeared at 3 m depth. At the same time the density of *Meyenaster gelatinosus* had more than doubled (to 1.4 ind. m⁻²) at 3 m depth. Observations during a dive at Bahía Cisnes in March 2007 also showed a marked change in the abundance of *H. helianthus*: it occurred only in low numbers in the rocky

Table 1. Results of 2-way ANOVAs testing for differences in the density of the 2 sea star species with Depth at each study location

Source	df	F	p
Flamenco			
Sea star	1	1.05	0.31
Depth	4	11.07	<0.0001
Sea star × Depth	4	7.54	<0.0001
Error	427		
Ramada			
Sea star	1	1.05	0.65
Depth	3	11.07	0.038
Sea star × Depth	3	7.54	0.0004
Error	244		
Bahía Cisnes			
Sea star	1	117.06	<0.0001
Depth	5	13.15	<0.0001
Sea star × Depth	5	15.36	<0.0001
Error	390		
Obispito			
Sea star	1	50.02	<0.0001
Depth	4	4.44	0.0018
Sea star × Depth	4	4.65	0.0013
Error	212		

zone and was absent in the sediment bottom zone. At the same time *M. gelatinosus* was more common throughout the rocky bottom zone.

Occurrence of *Heliaster helianthus* with autotomized arms

At Flamenco, the proportion of *Heliaster helianthus* with autotomized arms increased from 30% in the intertidal zone to ~60% in the upper subtidal zone (Fig. 4). At Ramada, the proportion of individuals with autotomized arms was already ~65% at 0 to 2 m depth and increased to ~90% at 2 to 6 m. In contrast, the proportion of *H. helianthus* with autotomized arms was low throughout the subtidal zone at Bahía Cisnes (22 to 29%) and even lower across the subtidal zone at Obispito (5 to 15%). A correlation analysis applied to the different depths and sites showed that the proportion of *H. helianthus* with autotomized arms was strongly correlated with the abundance of *Meyenaster gelatinosus* ($r_s = 0.72$, $p = 0.012$).

Feeding of *Heliaster helianthus* and *Meyenaster gelatinosus*

The percentage of *Heliaster helianthus* feeding was generally low at the 2 sites where *Meyenaster gelatinosus* was common. At Flamenco, although 56% of individuals fed in the upper subtidal zone (0 to 3 m), none fed at greater depths. The main prey consumed in shallow water were the mussel *Semimytilus algosus* (54%) and barnacles (17%). At Ramada, only 33 to 35% of the individuals fed across the subtidal zone (Fig. 4) and the main prey were the mussel *S. algosus* (21%) and the turban snail *Tegula* spp. (34%). In contrast, the percentage of *H. helianthus* feeding increased with depth at the locations where there were few *M. gelatinosus*. At Bahía Cisnes, it increased from 38% in the upper subtidal zone (0 to 2 m) to 92% in the sediment zone, and at Obispito from 37 to 89% over the same depth range. In the upper subtidal zone, the urchin *Tetrapygus niger* was the main prey at Bahía Cisnes (57%) and the mussel *S. algosus* at Obispito (38%). In the sediment zone, the gastropod *Turritella cingulata* was the main prey at both sites (93 and 86%, respectively). A correla-

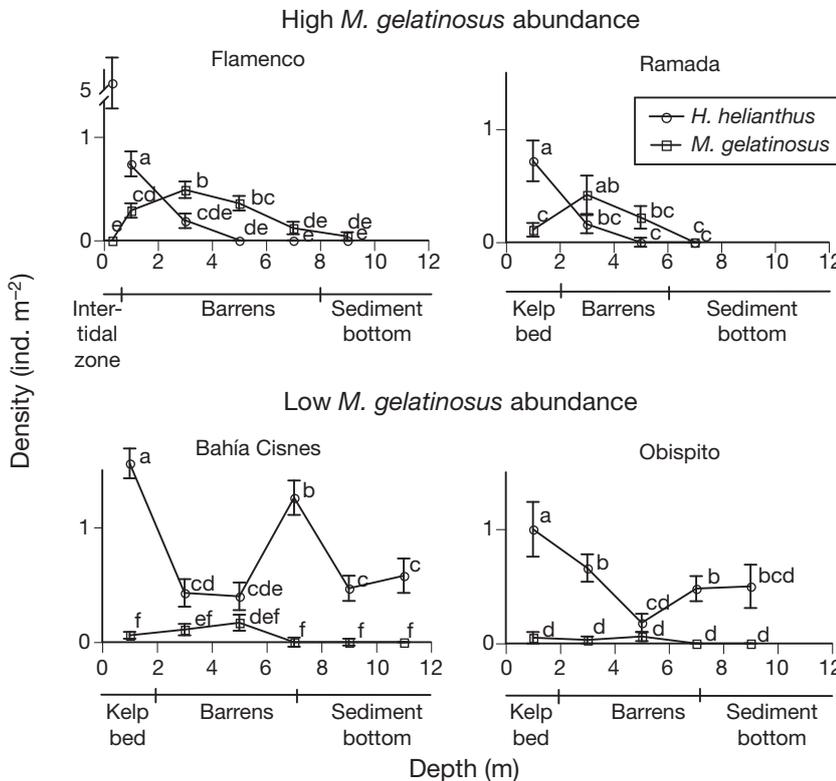


Fig. 2. *Heliaster helianthus* and *Meyenaster gelatinosus*. Abundance in relation to depth at 4 locations, 2 with high and 2 with low abundance of *M. gelatinosus*. Error bars represent \pm SE. For each species, values not sharing the same letters are significantly different

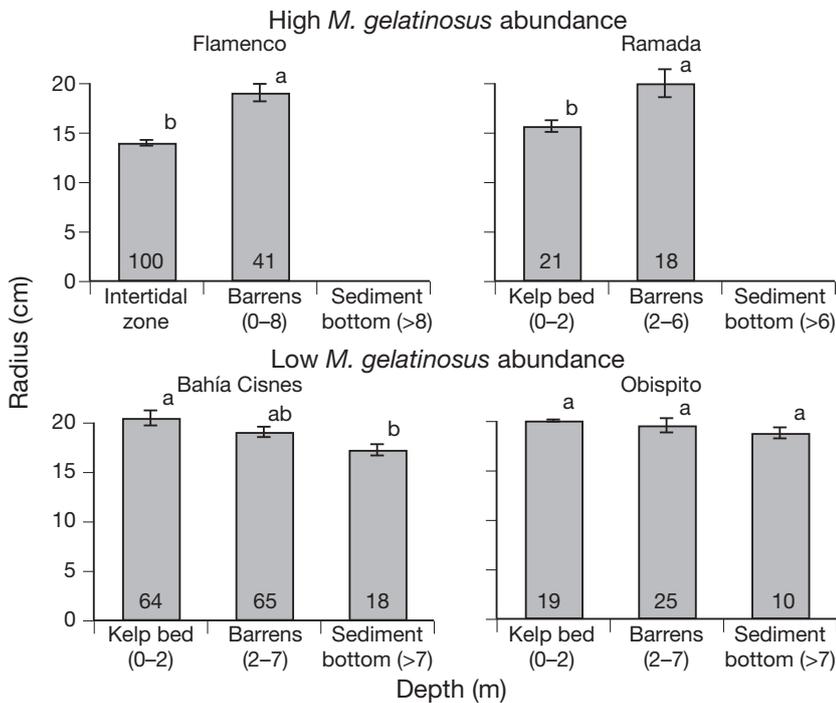


Fig. 3. *Heliaster helianthus* and *Meyenaster gelatinosus*. Average size of *H. helianthus* in different subtidal zones at locations with high and low abundance of *M. gelatinosus*. Sample size is indicated within the bar for each zone. Error bars represent \pm SE. Values not sharing the same letters are significantly different

tion analysis applied to the different depths and locations showed that the proportion of *H. helianthus* feeding was negatively correlated with the abundance of *M. gelatinosus* ($r_s = -0.60$, $p = 0.049$).

The main prey items consumed by *Meyenaster gelatinosus* were the sea urchin *Tetrapygus niger* (30% of the prey items observed at the 4 locations) and *Heliaster helianthus* (22% for the 4 locations together, but 39 to 42% at Bahía Cisnes and Ramada). Yule's V selectivity index showed that both prey were selected by *M. gelatinosus* (Table 2). The frequency of the sea urchin in the diet of *M. gelatinosus* varied with its availability. At Flamenco and Ramada, where *M. gelatinosus* was common, both the density of the sea urchin (6.3 and 0.1 m^{-2} , respectively) and its frequency in the diet of *M. gelatinosus* were low (8 and 18%, respectively). In contrast, at Bahía Cisnes and Obispito, where there were few *M. gelatinosus*, both the density of the urchins (20 ind. m^{-2} at both locations) and their frequency in *M. gelatinosus*' diet were increased (27 and 65%, respectively).

Effect of *Meyenaster gelatinosus* on the behavior of *Heliaster helianthus* in the field

Heliaster helianthus responded in a characteristic way to make contact with *Meyenaster gelatinosus* (Table 3). About 22 s after the initial contact, the arms that were touched began to move. Then at about 40 s, all arm tips were raised so that the body resembled a crown (Fig. 1). At this point the tube feet did not appear to be attached to the bottom. After about 69 s, the *H. helianthus* began to move away from *M. gelatinosus*. The mean time for separation from *M. gelatinosus* was slightly more than 2 min.

The *Meyenaster gelatinosus* that were added to the center of our 7 m^2 circular experimental plots generally moved in straight lines, but in no specific direction, out of the plots. This resulted

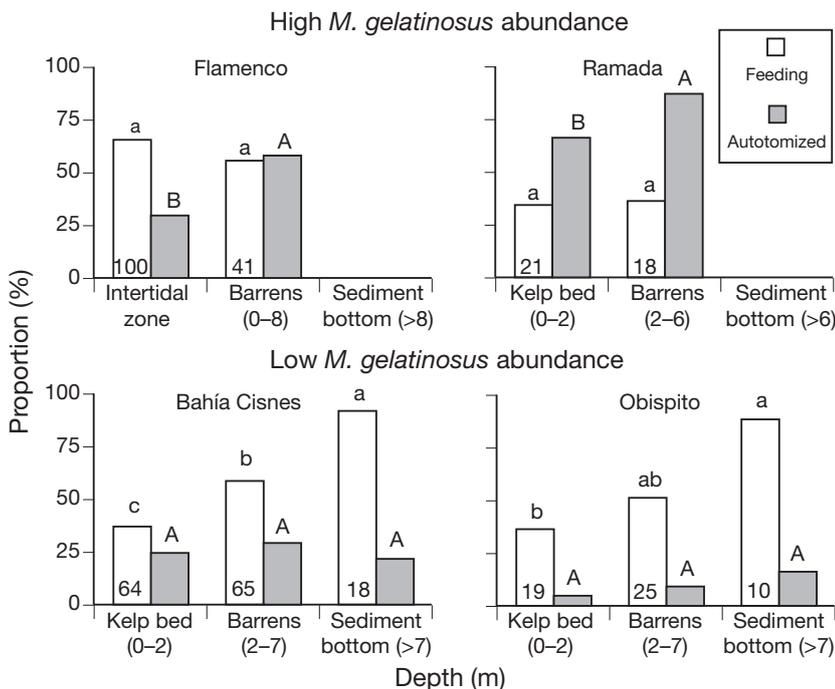


Fig. 4. *Heliaster helianthus* and *Meyenaster gelatinosus*. Proportion of *H. helianthus* feeding (white bars) and showing arm autotomy (grey bars) in different subtidal zones at locations with high and low abundance of *M. gelatinosus*. Sample size is indicated within the white bar for each zone. Values not sharing the same letters are significantly different

Table 2. *Heliaster helianthus* and *Meyenaster gelatinosus*. Yule's *V* prey selectivity index for different depth zones at Flamenco and Bahía Cisnes. ***p* < 0.01; **p* < 0.05; na: not available

Prey	Flamenco		Bahía Cisnes		
	Depth (m)		Depth (m)		
	<3	3-6	<2	2-7	>7
<i>H. helianthus</i>					
<i>Tetrapygyus niger</i>	-0.007	-0.000	-0.266	0.016	na
Barnacles	-0.042**	-0.001	-0.022	-0.004	na
<i>Semimytilus algosus</i>	0.045**	-0.000	0.508**	na	na
<i>Tegula</i> spp.	-0.007	-0.009	na	-0.008	na
<i>Pyura chilensis</i>	-0.011	-0.001	-0.055	-0.010	-0.000
<i>Turritella cingulata</i>	na	-0.002	0.190**	0.002	0.000
<i>Calyptrea trochiformis</i>	na	0.177**	na	na	na
<i>Fissurella</i> spp.	-0.003	-0.000	-0.022	na	na
<i>M. gelatinosus</i>					
<i>Tetrapygyus niger</i>	0.254**	0.364**	-0.303**	0.151**	na
Barnacles	-0.016	0.003	-0.033	-0.002	na
<i>Semimytilus algosus</i>	-0.072**	-0.028**	na	na	na
<i>Tegula</i> spp.	-0.004	-0.000	na	-0.003	na
<i>Pyura chilensis</i>	-0.004	-0.000	-0.023	-0.004	na
<i>Turritella cingulata</i>	na	-0.001	na	-0.138**	na
<i>Calyptrea trochiformis</i>	0.242**	na	0.497**	na	na
<i>Fissurella</i> spp.	0.148**	0.067**	-0.009	na	na
<i>Heliaster helianthus</i>	0.235**	0.302**	0.202**	0.276**	na

in random contacts with *Heliaster helianthus*. All contacts ultimately led to the fleeing of *H. helianthus*, leaving the experimental area in the direction opposite to that of the initial contact with *M. gelatinosus*. At times when a fleeing *H. helianthus* came into contact with conspecifics, it triggered an escape response in others, causing a localized stampede. This was not seen when a moving *H. helianthus* that was not fleeing *M. gelatinosus* came into contact with conspecifics. After 80 min in our trials in the circular plots, 96% of *H. helianthus* had fled the plots where *M. gelatinosus* had been added, which compared with only 4% in the plots where no *M. gelatinosus* had been added (Table 4, Fig. 5).

Prior to the *Meyenaster gelatinosus* additions to the circular plots, ~90% of the *Heliaster helianthus* were feeding (Fig. 6). The proportion dropped to ~40% in plots where *M. gelatinosus* was added, but did not change in the plots where no *M. gelatinosus* were added.

Table 3. *Heliaster helianthus* in response to contact with *Meyenaster gelatinosus* (n = 43)

	Average time (s)	SE
First response	21.6	3.3
Crown position (all arms raised)	39.7	6.1
Beginning to move away	68.7	10.6
Separated from <i>M. gelatinosus</i>	133.9	23.3

Table 4. Results of a 2-way ANOVA testing for differences between control and *Meyenaster gelatinosus* addition areas (Treatment) in the proportion of *Heliaster helianthus* that left the circular areas at different times (Time)

Source	df	F	p
Treatment	1	369.60	<0.0001
Time	7	9.84	<0.0001
Treatment × Time	7	6.67	<0.0001
Error	88		

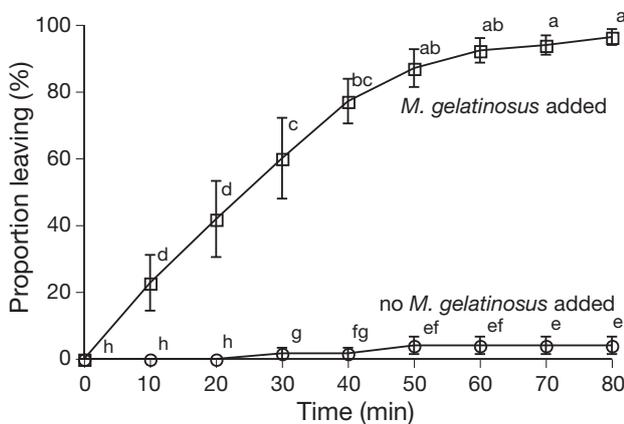


Fig. 5. *Heliaster helianthus* and *Meyenaster gelatinosus*. Proportion of *H. helianthus* leaving 3 m diameter circular plots in which we either added or did not add *M. gelatinosus*. Error bars represent ±SE. Values not sharing the same letters are significantly different

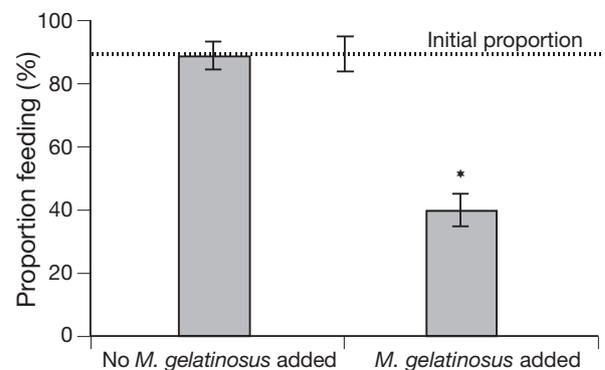


Fig. 6. *Heliaster helianthus* and *Meyenaster gelatinosus*. Initial proportion of *H. helianthus* feeding in circular experimental areas (dashed line) compared to the proportion feeding in areas where we added or did not add *M. gelatinosus* (bars). *Significant difference between the treatment and the initial proportion feeding (*p* < 0.05). Error bars represent ±SE

DISCUSSION

Our study provides several lines of evidence indicating a strong predatory impact of *Meyenaster gelatinosus* on *Heliaster helianthus*. First, *H. helianthus* was commonly eaten by *M. gelatinosus*, and Yule's *V* selectivity index indicated that *M. gelatinosus* selects *H. helianthus*. The high frequency of *H. helianthus* in the diet of *M. gelatinosus* was surprising because it is a large and very mobile prey. Second, our field surveys show an inverse relationship in the abundance of the 2 sea stars. At sites with low *M. gelatinosus* densities, *H. helianthus* occurred across the rocky subtidal zone and also into the sediment zone, whereas at sites with high *M. gelatinosus* densities, *H. helianthus* was only found in the intertidal and upper subtidal zones (Fig. 7). Nevertheless, we did not detect a small-scale segregation of the 2 sea stars (in the analysis of 1 m² sampling quadrats), as reported between 2 competing subtidal sea stars *Leptasterias polaris* and *Asterias vulgaris* in the northern Gulf of St. Lawrence (Gaymer et al. 2001). It is unlikely that avoidance at the scale of 1 m⁻¹ would reduce predatory attacks by *M. gelatinosus*, given that *M. gelatinosus* moves rapidly (up to 1.8 cm s⁻¹; Viviani 1978) and can probably detect prey from a distance (as

documented for numerous sea stars; Sloan & Aldridge 1981, Rochette et al. 1994, Drolet & Himmelman 2004). The third index of the predatory impact of *M. gelatinosus* on *H. helianthus* was provided by the frequency of *H. helianthus* with autotomized arms (as reported for the sea stars *Marthasterias glacialis* and *A. rubens*; Ramsay et al. 2000). These mainly result from attacks by *M. gelatinosus* (Viviani 1978). The frequency of *H. helianthus* with autotomized arms was lower (5 to 29%) across the rocky subtidal zone at locations with few *M. gelatinosus*, whereas it was higher and increased with depth at locations where *M. gelatinosus* was common (Fig. 7). The fourth observation indicating a predatory impact of *M. gelatinosus* was that the proportion of *H. helianthus* feeding was negatively related to the abundance of *M. gelatinosus*. At sites with few *M. gelatinosus*, the proportion of *H. helianthus* feeding increased with increasing depth (in part related to greater prey availability with increasing depth), whereas at sites where *M. gelatinosus* was common, the proportion was low and did not vary with depth (Fig. 7).

Our field experiments demonstrated a strong and unique escape response of *Heliaster helianthus* when touched by *Meyenaster gelatinosus*. *H. helianthus* took the 'crown' position, which involved raising the arm tips and detaching from the substratum (this occurred about 40 s after the initial contact), and then fleeing. The average time taken by *H. helianthus* to become separated from the predator was 2 min. The sudden raising of the arms could serve to detach *H. helianthus* from a pursuing *M. gelatinosus*. Also, we observed that when there was strong wave action a *H. helianthus* in crown position could be carried away from its predator. Similarly, Dayton et al. (1977) reported that urchins *Tetrapygus niger* fleeing from sea star predators are less well attached and can be carried away by wave action. We noted that when a fleeing *H. helianthus* touched conspecifics, there appeared to be communication between the first individual touched and the others, causing a stampede away from the predator. This possibly involves an alarm signal, such as that employed by some gastropods (Yamada et al. 1998) and sea urchins (Hagen et al. 2002) when threatened by their predators.

Attacks by *Meyenaster gelatinosus* are often non-lethal. Nevertheless, sublethal predation (i.e. loss of arms) could have a considerable impact, as it may lead to decreases in mobility and feeding, and consequently reduced energy storage and growth (Lawrence & Vásquez 1996, Díaz-Guisado et al. 2006, Naya & Bozinovic 2006). Although sublethal predation clearly leads to decreased fitness in many species (see Maginnis 2006), it is rarely incorporated into predator-prey models (for an exception see Zajac 1995). Rather, most

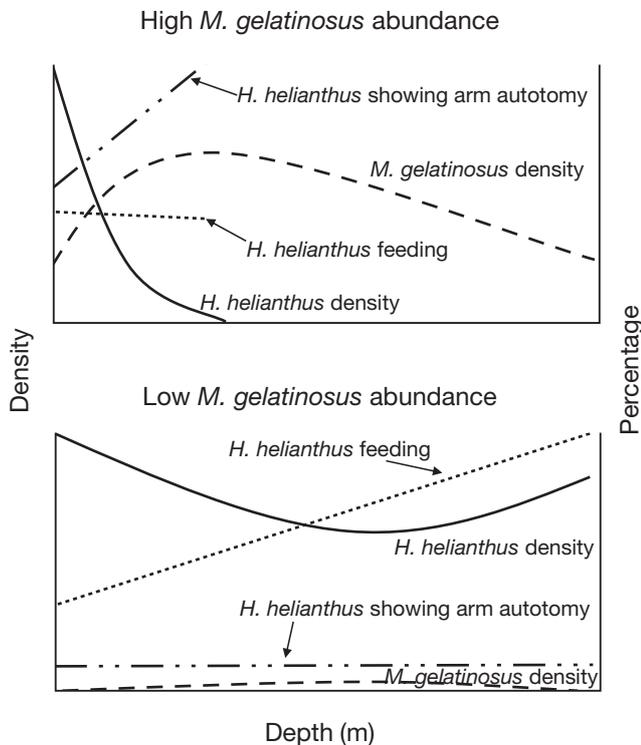


Fig. 7. *Heliaster helianthus* and *Meyenaster gelatinosus*. Generalized scheme of the depth distribution, and percentage of individuals feeding and showing arm loss (autotomy), for *H. helianthus* at locations with high and low abundance of *M. gelatinosus*

studies evaluate the effect of autotomy on the individual or population, but not on species interactions involving the autotomized species (see Maginnis 2006). The present study suggests that sublethal predation on *Heliaster helianthus* alters the role of this species in structuring the community. Recent studies in rocky intertidal communities in the Gulf of Maine indicate that the roles of the grazing snail *Littorina littorea* and the predatory snail *Nucella lapillus* are greatly reduced when these snails are exposed to the odor of a major predator, the green crab *Carcinus maenas* (Trussell et al. 2003, 2004). These sublethal effects, named trait-mediated indirect interactions, are passed on through a trophic cascade and result in an increased abundance of algae and prey species (Trussell et al. 2006).

Our observations indicate that *Meyenaster gelatinosus* can limit *Heliaster helianthus*' access to the extremely abundant prey *Turritella cingulata*. This gastropod covered the sediment bottom at Bahía Cisnes at a density of ~ 3000 ind. m^{-2} in 2003. Individuals were piled on top of one another to a depth of 5 to 10 cm (Fig. 2). Laboratory trials (C. F. Gaymer unpubl. data) showed that *H. helianthus* can consume 3 average-sized (~ 3 cm in length, or 1 g in tissue mass) *T. cingulata* d^{-1} . At this rate, the 1.3 *H. helianthus* m^{-2} observed at Bahía Cisnes in 2003 could consume 4 *T. cingulata* $m^{-2} d^{-1}$ (~ 1460 g $m^{-2} yr^{-1}$, equivalent to 49% of the standing crop in a year). Although many factors affect feeding rates (e.g. laboratory vs. field conditions, season), a high impact is also indicated by the high proportion of dead *T. cingulata* (42%) observed when we returned to Bahía Cisnes in 2006. The deeper environment where *T. cingulata* is found should allow almost continuous feeding by *H. helianthus*, in contrast to shallow habitats, where sea star feeding is likely reduced by wave activity (Sousa 2001, Gagnon et al. 2003).

Whereas both *Heliaster helianthus* and *Meyenaster gelatinosus* are adapted to living throughout the rocky subtidal zone, our observations indicate that *H. helianthus* is often restricted to shallow depths because of the predatory impact of *M. gelatinosus*. Many benthic species are similarly limited to shallow depths because of consumer pressure, notably benthic macrophytes by sea urchins (Lawrence 1975, Himmelman et al. 1983) and mussels by sea stars (Gaymer et al. 2001, Gaymer & Himmelman 2002). Smaller *H. helianthus* appear to be limited to even shallower depths (including the intertidal zone), probably because they are even more vulnerable to attacks by *M. gelatinosus* (they are likely slower at fleeing and more easily completely consumed because of their small size). *H. helianthus* recruits at shallow depths (Viviani 1978), which may represent an adaptation to avoid the predation threat of *M. gelatinosus*.

Studies are required to evaluate the roles of *Heliaster helianthus* and *Meyenaster gelatinosus* in determining the structure of subtidal communities in Chile. Paine et al. (1985) described *H. helianthus* as a keystone predator in intertidal communities in central Chile. The high numbers of this generalist predator at shallow depths suggests that its feeding could similarly have a strong impact on upper subtidal prey species, such as turban snails *Tegula* spp., keyhole limpets *Fissurella* spp. and barnacles. *H. helianthus* also preys on the whelk *Concholepas concholepas* (called the 'loco' in Chile), which Castilla & Duran (1985) described as another keystone predator in intertidal communities. Thus, *H. helianthus* may also have a strong impact throughout the rocky subtidal zone, and even into the sediment zone, at locations where there are few *M. gelatinosus*. As the 'loco' is overexploited in most rocky communities in Chile, except in a few areas where humans are excluded, *H. helianthus* is left as the only recognized keystone intertidal predator (Navarrete & Castilla 2003). However, the 'loco' populations should increase if the newly created marine protected areas (MPAs) along the coast of northern and central Chile succeed in preventing them from being harvested.

The predatory impact of *Heliaster helianthus* is undoubtedly greatly reduced in communities where *Meyenaster gelatinosus* is common or abundant. *M. gelatinosus* also presents a predatory risk for the 'loco' *Concholepas concholepas*, which responds with both an escape response and reduced feeding (Serra et al. 1997). Thus, it is more likely that *M. gelatinosus*, rather than *H. helianthus* or *C. concholepas*, is the keystone predator in Chilean rocky subtidal communities. In present-day communities in Chile, *M. gelatinosus* may be at the top of a trophic cascade (sensu Estes et al. 1998). The situation may have been different at an earlier time, as the impact of a number of large predatory fishes has been reduced by overfishing. These include *Graus nigra* and *Primelometopon maculatus*, which are known to prey on sea stars (Fuentes 1982). Studies are needed to quantify the role of *M. gelatinosus* in structuring subtidal communities, for example by following manipulations of its numbers. Most rocky surfaces, in both areas with high and low *M. gelatinosus* densities, are covered by barrens with extensive cover by crustose coralline algae but few fleshy macrophytes. The most conspicuous grazer, the black sea urchin *Tetrapygus niger*, is a major prey of both *M. gelatinosus* and *H. helianthus*. However, as *H. helianthus* is a generalist predator, whereas *M. gelatinosus* prefers echinoderms (Aburto 1999 and Table 2), one might predict that a shift from *H. helianthus* to *M. gelatinosus* would lead to a reduction in urchin numbers and impact. A negative impact of *M. gelatinosus* on urchins was also suggested by our field data for locations with high and low

M. gelatinosus abundance. In the upper sediment zone, we expect that high densities of *Turritella cingulata* can only develop when *H. helianthus* is excluded by *M. gelatinosus*. *M. gelatinosus* virtually does not feed on *T. cingulata*. In turn, high densities of *T. cingulata* likely limit numbers of infaunal and epifaunal species. We predict that the recent disappearance of *H. helianthus* from the sediment zone at Bahía Cisnes (in 2007) will now allow *T. cingulata* numbers to increase.

It is likely that numbers of *Meyenaster gelatinosus* and *Heliaster helianthus* are not specific to particular sites but change over time. We detected changes within 2 yr at both Bahía Cisnes and Flamenco. Shifts are probably first caused by a change in the numbers of *M. gelatinosus*, which consequently changes the numbers of *H. helianthus*. We have a poor understanding of the factors controlling the distribution of *M. gelatinosus*. Its morphology (Fig. 1) would suggest that it is poorly adapted to withstanding the strong wave action often characteristic of shallow subtidal areas. For example, its large size (up to 50 cm) and relatively thick arms likely create resistance to waves. In contrast, *H. helianthus*, even though it can be large (up to 32 cm), is thinner (Fig. 1) and more closely adheres to rocky surfaces, thus reducing resistance to water movement. Its many arms and large numbers of podia should also enhance attachment. Finally, its body wall is more robust than that of *M. gelatinosus* (which is soft), so that it should be less vulnerable to damage from moving objects. Studies are needed to elucidate factors causing changes in *M. gelatinosus* populations over time.

Certain predators may be 'keystones' in specific habitats, but their role may change in other habitats, even adjacent habitats (Power et al. 1996), and this seems to be the case for *Heliaster helianthus*. We have documented that the predatory role of *H. helianthus* in rocky coastal communities in Chile can be greatly reduced in the rocky subtidal zone by a higher-order predator, *Meyenaster gelatinosus*, which limits its numbers, foraging activities and access to prey.

Acknowledgements. We are grateful to J. Barrios and A. Vega for their help in sampling in the field. C. P. Dumont, M. Thiel and P. S. Petraitis made useful suggestions for improving the paper. The study was supported by a Fondo Nacional de Desarrollo Científico y Tecnológico (FONDECYT, Chile) grant (#3030007) to C.F.G.

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Editorial responsibility: Charles Peterson,
Morehead City, North Carolina, USA

Submitted: November 19, 2007; Accepted: July 23, 2008
Proofs received from author(s): October 18, 2008