

Feeding habits of two deep-sea sharks from central-northern Chile: hooktooth dogfish *Aculeola nigra* (Etmopteridae) and dusky catshark *Bythaelurus canescens* (Scyliorhinidae)

Hábitos alimentarios de dos tiburones de profundidad del centro-norte de Chile: tolo negro de cachos *Aculeola nigra* (Etmopteridae) y pejegato oscuro *Bythaelurus canescens* (Scyliorhinidae)

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Abstract. - Feeding habits of 381 specimens of *Aculeola nigra* and 513 specimens of *Bythaelurus canescens* were studied. In 121 stomachs of *A. nigra* and 312 of *B. canescens* preys were found. Individuals were collected as by-catch from the deep-sea crustacean fishery, between 25°20'S and 35°43'S; from January 1997 to July 2000 off the northern-central Chilean coast. The most important prey by index of relative importance and by frequency of occurrence in *A. nigra* was the benthic deep-sea shrimp *Heterocarpus reedi*; while by number the euphausiid *Euphausia mucronata* and by weight the common hake *Merluccius gayi* were the most important. The deep-sea shrimp *H. reedi* was also the most important prey of *B. canescens*, for all feeding indices used. Significant differences were found in the habitat where these predators consume their prey, *A. nigra* eating more on pelagic prey; whereas *B. canescens* feeds more on benthic prey. *A. nigra* showed a higher trophic niche breadth, because they predate more on benthic, pelagic and mesopelagic resources; whereas *B. canescens* feeds primarily on benthic prey. The diet of both species significantly overlapped, suggesting a high competition between them.

Key words: By-catch, pelagic, benthic, trophic niche breadth, trophic overlap

INTRODUCTION

The biology of deep-sea sharks is poorly known compared to that of their shallower-waters relatives, although deep-sea sharks are important top predators occupying a high trophic level (Cortés 1999). Therefore the study of deep-sea sharks distribution, biology and ecology is essential to better understand the dynamics of communities inhabiting this environment. According to Gartner *et al.* (1997) the largest predators in the deep-sea are sharks, but only the smaller shark species have been well studied.

Recent efforts have been made to study the biodiversity, life history and fisheries of deep-sea chondrichthyans, but the understanding of deep-sea fauna is considerably behind the level of knowledge of some inshore and pelagic chondrichthyans (Kyne & Simpfendorfer 2007). Knowledge of deep-sea sharks in the Southeastern Pacific Ocean off Chile is restricted mainly to taxonomy, systematic and distribution (Compagno 1984, Meléndez & Meneses 1989, Pequeño 1989), while their reproduction and feeding habits have been poorly described (Burgess & Springer 1986, Arancibia & Meléndez 1987).

Determining the trophic relationships among species helps understanding their community organization and effect on their ecosystem (Krebs 1989). The trophic relationships between marine organisms are complex, involving different intra and inter-specific strategies for occupying separate ecological niches to partition food resources and this allows exploitation of different resources and habitats (Hyndes *et al.* 1997). This kind of research has been described for three shark species and a ray in nearshore waters of a large subtropical embayment (White *et al.* 2004), and in four carcharhinid sharks around the Hawaiian Islands (Papastamatiou *et al.* 2006).

Chondrichthyan fishes are by-catched in the deep sea shrimp trawl fishery along central-northern Chile. They comprise 9.28% by weight of by-catched fishes and include at least ten shark, four ray and one chimaerid species, but only two shark species are relatively important in the catch, the hooktooth dogfish *Aculeola nigra* and the dusky catshark *Bythaelurus canescens*, which account for 49% and 20.3% of the chondrichthyans, respectively (Acuña & Villarroel 2002).

Aculeola nigra de Buen, 1959 (Etmopteridae) is found only in the southeastern Pacific Ocean between Trujillo, Perú (7°49'S) and Constitución, Chile (35°26'S); on the continental shelf and upper slope between 110 and 735 m depth (Meléndez & Meneses 1989). *Bythaelurus canescens* Günther, 1878 (Scyliorhinidae) is distributed from Southern Ecuador to the Strait of Magellan (Compagno 1984). Its bathymetric distribution ranges between 250 and 1,260 m depth (Meléndez & Meneses 1989). Both species are particularly abundant below 300 m depth, as indicated by catches in the deep-sea shrimp *Heterocarpus reedi* fishery (González 2001). However, although they occupy the same spatial distribution, several aspects on their ecology have not been studied. The aim of this study is to describe the feeding habits; trophic niche breadth and diet overlap of these two species.

MATERIAL AND METHODS

Specimens of the deep-sea sharks *A. nigra* and *B. canescens* were obtained between February 1997 and July 2000 from by-catch of the deep-sea shrimp fishery existing between 25°20'S and 35°43'S. Depth of sampling ranged between 115 and 480 m. Sharks were retained on ice onboard the vessel, and then taken to the laboratory for further analysis. Subsequently, specimens were sexed and measured (nearest 1 mm TL). Stomachs were extracted and preserved in 10% formalin. The stomachs were dissected and all prey items identified to the lowest possible taxa using classifications from Roper *et al.* (1984) for Cephalopoda, Manning (1968) for Stomatopoda, Retamal (1994) for Decapoda, Mauchline & Fisher (1969) for Euphausiacea and Nelson (1994) for Teleostei. Prey items were counted and their total wet weight was determined.

The minimum number of stomachs to be analyzed by species was estimated using the cumulative prey curves obtained from randomly pooled subsets of stomachs of each species according to Cortés (1997).

The numeric (N), gravimetric (W), frequency of occurrence (FO) (Cortés 1997) and relative importance (IRI) indices (Pinkas *et al.* 1971) were used for the analysis of feeding habits.

Similarity percentages were used to determine which prey items characterized the diets of each species and made the highest contributions to dissimilarities between both species (Clarke 1993). PRIMER v5 (Clarke & Gorley 2001) was used on each dietary indices described above.

The IRI was used to determine trophic niche-breadth for each species by means of the Shannon-Wiener index (H') (Krebs 1989) and is expressed as:

$$H' = -\sum p_j \log p_j$$

Where H' is the Shannon-Wiener measure of trophic niche-breadth and p_j is the proportion of the IRI. A high H' value indicates feeding on a higher spectrum width of prey-items.

The Shannon-Wiener measure H' was standardized on a 0-1 scale using the evenness measure J' which is expressed as:

$$J' = \frac{H'}{\log n}$$

Where J' is the evenness measure of the Shannon-Wiener function and n is the total number of prey items. A high J' indicates a fish feeding on a relatively larger number of a few main prey types (Shuozeng 1995).

The degree of trophic overlap between species was estimated by means of the simplified Morisita index (C) (Krebs 1989). The value of C varies from 0 for no overlap to 1 for complete overlap, with a value of ≥ 0.6 being considered to be significant (Hyndes *et al.* 1997). This measure is expressed as:

$$C = \frac{2\sum p_{ij} p_{ik}}{\sum p_{ij}^2 + \sum p_{ik}^2}$$

Where C is the simplified Morisita index of trophic niche overlap between species j and k and p_{ij} and p_{ik} are the proportion of prey-item i consumed by species j and k , respectively.

RESULTS

A total of 381 specimens of *A. nigra* and 513 specimens of *B. canescens* were collected during this study. The size-frequency distribution of *A. nigra* showed that the mode for males was around 45 cm total length (TL), while the mode for females was at 50 cm TL. Both sexes of *B. canescens* had a smallest mode at around 30 cm TL (Fig. 1).

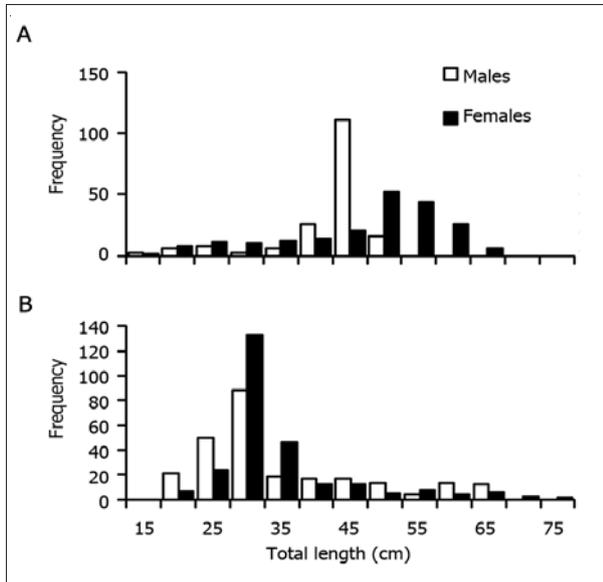


Figure 1. Size-frequency distribution by sex for; A) *Aculeola nigra* and B) *Bythaelurus canescens*, obtained from by-catch of the deep-sea shrimp fishery between 1997 and 2000 / Distribución de frecuencia de tallas, por sexo de A) *Aculeola nigra* y B) *Bythaelurus canescens* obtenidos como fauna asociada a la pesquería de camarón nailon entre 1997 y 2000

The minimum sample size of stomachs to study feeding habits of these species using cumulative prey curves was determined to be 24 stomachs for *A. nigra* and 26 stomachs for *B. canescens* (Fig. 2).

In *A. nigra*, the most important prey species by number was the euphausiid *Euphausia mucronata*, followed by the myctophid *Diogenichthys laternatus*, both pelagic preys. By weight the most important *A. nigra* identified prey was the hake *Merluccius gayi*. However, according to the frequency of occurrence and relative importance indices, the benthic prey *Heterocarpus reedi* was the single most important prey item of this species.

Heterocarpus reedi was also the most important prey of *B. canescens*, by number, weight, frequency of occurrence and relative importance indices. For both species a high percentage of unidentified fishes, crustacean and digested remains were found. *Aculeola nigra* had a high percentage by number of pelagic preys in its diet, being also important by weight, occurrence and relative importance (20.6%, 11.1% and 13.7%, respectively). *Bythaelurus canescens* feeds mainly upon benthic prey by number, weight, frequency of occurrence and relative importance, while pelagic prey showed percentages between 0.2 and 3.7% (Table 1). Chunks of saury *Scomberesox saurus* and rattail fish *Nezumia pulchella*

were also found in two and one stomach of *A. nigra*, respectively.

An average dissimilarity of 46.51% was obtained when using the numeric index (%N), with *E. mucronata* contributing with the highest percentage, followed by *D. laternatus* and *H. reedi* (Table 2). When using %W the average dissimilarity was 41.6%, with *D. laternatus* contributing with the highest percentage, followed by *M. gayi* and mud as a dietary category as in Carrasson *et al.* (1992) and White *et al.* (2004). An average dissimilarity of 29.27% was obtained when using the frequency of occurrence index (%FO), with mud contributing with the highest percentage, followed by *D. laternatus* and unidentified cephalopods and *Lophorochinia parabranchia* (Table 2). Finally, when using % IRI the average dissimilarity was 37.29% with *D. laternatus* contributing with the highest percentage, followed by mud, unidentified cephalopods and *H. reedi* (Table 2). A trophic niche breadth of $H' = 3.01$ and an evenness index of $J' = 0.68$ were estimated for *A. nigra*, parameters which were higher than for *B. canescens*, where $H' = 2.34$ and $J' = 0.52$ were found. Feeding of both species showed a significant overlap of 80%.

DISCUSSION

Stevens *et al.* (2000) pointed out that when sharks are taken as by-catch, they are often subject to high fishing mortality and may be virtually eliminated from large regions altering size structure and population parameters. This can

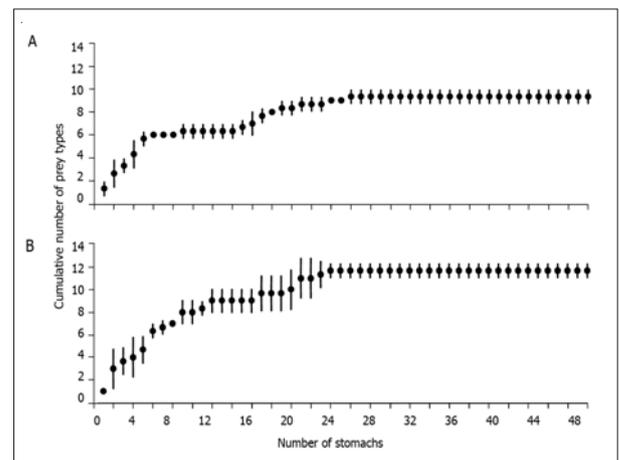


Figure 2. Cumulative prey curves for A) *Bythaelurus canescens* and B) *Aculeola nigra*. Bars show standard error for three mean randomly pooled stomach sets / Curva acumulativa de presas de A) *Bythaelurus canescens* y B) *Aculeola nigra*. Las barras muestran el error estandar de tres grupos promedio de estómagos conformados al azar

Table 1. Prey-item, prey type, percentage by number (%N), weight (%W), frequency of occurrence (%FO) and index of relative importance (%IRI) for *Aculeola nigra* and *Bythaelurus canescens*. Maximum values are in bold / Ítem presa, Tipo de Presa, Porcentaje numérico (%N), gravimétrico (%W), frecuencia de ocurrencia (%FO) índice de importancia relativa (%IRI) para *Aculeola nigra* y *Bythaelurus canescens*. Los valores máximos se muestran en negrita

Prey-item	Prey type	<i>A. nigra</i>				<i>B. canescens</i>			
		%N	%W	%FO	%IRI	%N	%W	%FO	%IRI
POLYCHAETA	Benthic					0.4	0.1	0.3	<0.1
MOLLUSCA									
Cephalopoda									
<i>Loligo gahi</i>	Pelagic	0.5	0.1	0.8	<0.1	0.9	0.1	0.6	<0.1
Unidentified cephalopods		5.9	4.0	8.3	5.5	1.3	0.3	1.0	0.1
CRUSTACEA									
Squillidae									
<i>Pterygosquilla armata</i>	Benthic	0.5	0.4	0.8	<0.1	4.4	3.2	2.9	0.9
Euphausiidae									
<i>Euphausia mucronata</i>	Pelagic	37.9	0.3	1.5	3.9	0.9	0.2	0.6	<0.1
Solenoceridae									
<i>Haliporoides diomedea</i>	Benthic					0.4	0.7	0.3	<0.1
Pasiphaidea									
<i>Pasiphaea acutifrons</i>	Pelagic					0.9	0.2	0.6	<0.1
Pandalidae									
<i>Heterocarpus reedi</i>	Benthic	11.3	8.9	15.8	21.6	37.1	27.1	17.6	45.3
Glyphocrangonidae									
<i>Glyphocrangon alata</i>	Benthic					2.6	2.6	1.3	0.3
Polychelidae									
<i>Stereomastis summi</i>	Benthic					0.4	0.4	0.3	<0.1
Galatheididae									
<i>Cervimunida johni</i>	Benthic	2.5	3.6	3.8	1.5	3.9	3.8	2.6	0.8
<i>Pleuroncodes monodon</i>	Benthic	4.4	4.0	5.3	3.0	5.7	6.2	4.2	2.0
Unidentified galatheids		0.5	0.2	0.8	<0.1	0.4	0.1	0.3	<0.1
Calappidae									
<i>Mursia gaudichaudii</i>	Benthic					1.7	1.8	1.3	0.2
Majidae									
<i>Lophorochinia parabranchia</i>	Benthic					4.8	2.7	3.5	1.1
Cancridae									
<i>Cancer porteri</i>	Benthic					0.9	0.9	0.3	<0.1
Unidentified crustaceans		4.4	1.7	6.8	2.8	10.5	8.2	7.7	5.8
Crustacean remains			1.4	7.5	0.7		9.9	19.2	7.6
TELEOSTEI									
Notosudidae									
<i>Scopelosaurus</i> sp.	Benthic	0.5	0.7	0.8	0.1				
Myctophidae									
<i>Diogenichthys laternatus</i>	Pelagic	15.3	7.1	4.5	6.8				
<i>Protomyctophum chilensis</i>	Pelagic	0.5	0.6	0.8	0.1				
<i>Lampanyctus iselinoides</i>	Pelagic	0.5	0.2	0.5	<0.1				
Unidentified myctophids	Pelagic	3.0	8.3	3.0	2.3	1.3	3.3	1.0	0.2
Macrouridae									
<i>Nezumia pulchella</i>	Benthic	0.5	0.6	0.8	0.1				
Merlucciidae									
<i>Merluccius gayi</i>	Benthic	0.5	11.1	0.8	0.6	0.4	0.7	0.3	<0.1
Scomberosocidae									
<i>Scomberosox saurus</i>	Pelagic	1.5	3.9	1.5	0.6				
Unidentified fishes		9.9	24.0	15	34.4	21.8	12.6	15.7	21.6
Fish remains			4.2	7.5	2.1		3.6	6.7	1.0
Digested remains			6.8	19.5	8.9		11.0	29.8	13.2
Mud(*)			8.0	9.0	4.9		0.2	0.3	<0.1
Total benthic prey		20.2	29.3	24.2	26.9	62.9	50.2	29.6	50.5
Total pelagic prey		59.1	20.6	11.1	13.7	3.1	3.7	1.9	0.2
Number of stomachs with food				121				312	
Total number of stomachs				381				513	

(*) included as dietary category as in Carrasson *et al.* (1992) and White *et al.* (2004).

Table 2. Contribution (Contrib %) to average dissimilarity by prey item and dietary index between *A. nigra* and *B. canescens*. Percentage by number (%N); weight (%W); frequency of occurrence (%FO) and index of relative importance (%IRI). The name of the Genus should be consulted on the Table 1 / Contribución (Contrib %) a la disimilaridad por ítem presa e índice dietario entre *A. nigra* y *B. canescens*. Porcentaje numérico (%N); gravimétrico (%W); frecuencia de ocurrencia (%FO) e índice de importancia relativa (%IRI). Para el nombre de los géneros se debe consultar la Tabla 1

%N		%W		%FO		%IRI	
Prey-item	Contrib %						
<i>E. mucronata</i>	16.51	<i>D. laternatus</i>	8.16	Mud	9.92	<i>D. laternatus</i>	11.23
<i>D. laternatus</i>	12.34	<i>M. gayi</i>	7.70	<i>D. laternatus</i>	8.61	Mud	9.28
<i>H. reedi</i>	8.52	Mud	7.21	Unidentified cephalopods	7.74	Unidentified cephalopods	9.03
<i>L. parabranchia</i>	6.89	<i>H. reedi</i>	6.82	<i>L. parabranchia</i>	7.50	<i>H. reedi</i>	8.95
<i>G. alata</i>	5.09	<i>S. saurus</i>	6.09	Crustacean remains	6.39	Crustacean remains	8.28
Unidentified fishes	4.78	Crustacean remains	6.06	<i>S. saurus</i>	4.97	<i>E. mucronata</i>	7.76
<i>P. armata</i>	4.35	<i>L. parabranchia</i>	5.07	<i>G. alata</i>	4.52	Unidentified fishes	5.23
<i>M. gaudichaudii</i>	4.15	<i>G. alata</i>	4.92	<i>M. gaudichaudii</i>	4.52	Unidentified myctophids	4.71
Unidentified cephalopods	4.08	Unidentified crustaceans	4.84	Digested remains	3.88	<i>L. parabranchia</i>	4.43
<i>S. saurus</i>	3.84	Unidentified cephalopods	4.42	<i>Scopelosaurus</i> sp.	3.52	<i>S. saurus</i>	3.19
Unidentified crustaceans	3.53	Unidentified fishes	4.14	<i>N. pulchella</i>	3.52	Unidentified crustaceans	3.13
<i>P. acutifrons</i>	2.94	<i>M. gaudichaudii</i>	4.09	<i>P. chilensis</i>	3.52	<i>P. armata</i>	3.12
<i>C. porteri</i>	2.94	<i>P. armata</i>	3.66	<i>L. iselinoides</i>	3.52	<i>M. gayi</i>	2.79
<i>Scopelasaurus</i> sp.	2.22	Unidentified myctophids	3.29	<i>P. armata</i>	3.27	Digested remains	2.74
<i>N. pulchella</i>	2.22	<i>C. porteri</i>	2.89	<i>P. acutifrons</i>	3.20	<i>G. alata</i>	2.22
<i>P. chilensis</i>	2.22	<i>Scopelasaurus</i> sp.	2.60	Unidentified myctophids	3.12	Fish remains	2.03
<i>L. iselinoides</i>	2.22	<i>H. diomedae</i>	2.59	Polychaeta	2.26	<i>M. gaudichaudii</i>	1.83
Polychaeta	2.08	<i>P. chilensis</i>	2.48	<i>H. diomedae</i>	2.26	<i>C. johni</i>	1.51
		<i>N. pulchella</i>	2.34	<i>C. porteri</i>	2.26		
		Digested remains	2.21	<i>S. suhmi</i>	2.26		
Pelagic	57.15	Pelagic	65.48	Pelagic	68.12	Pelagic	73.53
Benthic	42.85	Benthic	34.52	Benthic	31.88	Benthic	26.47

be the result either of direct mortality due to fishing and/or post-release mortality, when the sharks are discarded. Most specimens of *B. canescens* captured comprised juveniles, while a significant part of the size structure of *A. nigra* was represented by adults. However, this may be well explained by the different depth range described for the two species and the depth range covered by this study; since our sampling covers most of the habitat of *A. nigra* and only the upper fourth of the depth range of *B. canescens*, while their adults have been found at deeper depths, in the Patagonian toothfish *Dissostichus eleginoides* fishery (Oyarzún *et al.* 2003).

Although Wetherbee *et al.* (1990) suggested that the occurrence of high proportions of empty stomachs in shark diet studies and in commercial fisheries operations is common, in our study this was confirmed only in *A. nigra*, with 32% of the stomachs with contents in general, and especially in males, where this percentage also clearly decreased with increasing sizes. On the other hand, *B. canescens* showed a higher percentage of stomachs with contents (61%, for all sizes) and also the percentage increased with size, in both sexes.

Some authors have reported an opportunistic behaviour in the feeding habits of some deep-sea sharks (Mauchline & Gordon 1983, Carrassón *et al.* 1992, Ebert *et al.* 1992) with species scavenging on fish carcasses (Bergstad *et al.* 2003). This behavior was observed in *A. nigra* feeding upon parts of prey such as *Nezumia pulchella* and *Scomberesox saurus*.

The diversity of diets of deep-sea sharks is characterized to consist of two groups of species. One feeding on relatively few prey classes and having a diet of low diversity and another one with more diverse diet and less restricted dietary composition (Mauchline & Gordon 1985). According to our results, specifically those of *H.*, *B. canescens* could be classified in the first category, while *A. nigra* in the second one.

Cortés (1999) in his analysis of the diet composition and trophic levels of several shark species, listed *A. nigra* as feeding mainly on decapod crustaceans and secondarily on fishes and cephalopods, although his data is based only in two specimens. In this study, the feeding habits of the species were confirmed, in terms of the kinds of prey,

although fishes were more important and also feeding on euphausiids was found in smaller specimens, suggesting that the species has benthic as well as pelagic feeding habits through its life. The presence of micronektonic crustaceans such as euphausiids and other vertical migrants suggests direct links between the epipelagic production and the deep-living species (Bergstad *et al.* 2003). In addition, the diet of other deep-sea sharks that eat upon pelagic macroplankton and micronekton suggests a generalized benthopelagic foraging behaviour (Neiva *et al.* 2006). Sharks showing this kind of behaviour, feed upon myctophids and other mesopelagic fish and nektonic species that have a closer relationship with the sediment interface, but not upon epi or endobenthic prey (Neiva *et al.* 2006). This type of diet and behavior is closer to what was found in *A. nigra*.

Other deep-sea sharks are mainly benthic top predator and also scavengers (Cherel & Duhamel 2004), such as species of the family Scyliorhinidae which show a diet composition based mainly in fishes and decapod crustaceans (Cortés 1999, Stergiou & Karpouzi 2002). This study showed that *B. canescens* feeds mainly on decapod crustaceans and secondarily on fishes, suggesting that this species has epibenthic feeding habits.

Studies on deep-sea megafaunal community have indicated that larger predators such as sharks have a low depth overlap within the same trophic guild, indicative of high depth zonation with no bathymetric substitution of species (Cartes & Carrassón 2004). One distribution pattern like this would explain the high trophic overlap of both species studied here. However, *A. nigra* has also diversified its trophic spectrum, exploiting pelagic prey and thus it has lowered the competition with *B. canescens* to a narrower depth range.

ACKNOWLEDGMENTS

We thank C. Vargas and P. Herrera for assistance in sample processing and all technical support of the Fisheries Laboratory at Universidad Católica del Norte-Coquimbo. The study was partially supported by fishing companies of Coquimbo and the Fisheries Research Fund (FIP), Chile. Editorial comments by John Stevens and two anonymous reviewers are deeply appreciated.

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Recibido el 20 de julio de 2009 y aceptado el 29 de mayo de 2010