THE NATURAL DIET OF THE GREEN ABALONE (HALIOTIS FULGENS PHILIPPI) IN THE SOUTHERN PART OF ITS RANGE, BAJA CALIFORNIA SUR, MEXICO, ASSESSED BY AN ANALYSIS OF GUT CONTENTS

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ABSTRACT An attempt was made to assess the natural diet of the green abalone from the southern extreme of its range by examination of gut contents. Crop and stomach contents were identified in samples from study sites at Bahía Asunción, La Bocana, Punta Abreojos, and Las Barrancas along the Pacific Coast of Baja California Sur. Shell lengths of abalone from banks at the northern sites, Bahía Asunción and La Bocana, were greater than for abalone found at the southern sites, Punta Abreojos and Las Barrancas. The consistency and weight of gut content among individuals varied according to the extent of digestion in each. Differences were found between the weight of the particulate contents at the different sites. The smallest number of plant species in the gut was one, and the largest was six. The average number of plant species per individual gut was similar at three sites. The highest average was at Las Barrancas. Seven Rhodophytes, four Phaeophytes, and one seagrass were recorded. The number of species in samples from Las Barrancas was nine, followed by Bahía Asunción (n = 8), La Bocana (n = 7), and Punta Abreojos (n = 5). The most common food items in gut content were the seagrass *Phyllospadix torreyi* and the macroalgae *Sargassum* sp., *Eisenia arborea, Cryptopleura crispa,* and *Rhodymenia* sp. The other species found in the abalone diets could be considered species that are consumed incidentally with the main food according to the local flora. The brown algae *Sargassum* and *Eisenia* and the red algae *Cryptopleura* and *Rhodymenia* made up about 50% (relative frequency) of the recovered food items at Bahía Asunción and Las Barrancas and about 80% at La Bocana and Punta Abreojos. *P. torreyi* formed 32% of the recovered food items at Punta Prieta and about 15% at the other sites. No other algae formed more than 12% of the gut content items in these green abalone.

KEY WORDS: natural diet, gut content, green abalone, Haliotis

INTRODUCTION

Seaweed plays an important role in nearshore marine ecosystems as a source of food, habitat, or refuge for many species of fauna, mollusks, crustaceans, and fish. In the wild, the common food of the adult abalone consists of macroalgae. Abalone food preferences have been studied from both analyses of gut contents and feeding experiments. Shepherd and Steinberg (1992) reviewed the literature on the feeding biology of abalone and found that although most populations have a wide range of acceptable algae for food, each species is fairly selective and usually has a preferred food item. Abalone have available to them different types of food in different parts of the world. In the northern hemisphere, there is a general preponderance of brown algae in the abalone diet. In the southern hemisphere, abalone feed mostly on the abundant red algae.

The benthic environments inhabited by abalone off southern California are characterized chiefly by Phaeophyta (brown algae). Dominant species include Macrocystis pyrifera (L.). C. Ag., Pelagophycus porra (Lem.) Setch., Laminaria farlowii Setch., Pterygophora californica Rupr., Egregia menziesii (Turn.) Aresh., Eisenia arborea Aresh., and Cystoseira osmundacea (Turn.) C. Ag. Rhodophyta (red algae) present generally include articulated and encrusting coralline algae, Rhodymenia spp., Gelidium spp., Gigartina spp., and Plocamium spp. (Dawson et al. 1960). Chlorophyta (green algae) do not form a conspicuous part of the algal flora of near-shore areas south of Point Conception (Leighton 1968). The production of Macrocystis, understory kelps, and bottom-cover algae, together with energy imported from the plankton, supports consumers in giant kelp forests as well as in nearby communities receiving drift from these beds or forests (Foster and Schiel 1985).

In California, the bull kelp, Nereocystis leutkeana (Mert.) Post. & Rupr.; giant kelp, Macrocystis; elk kelp, Pelagophycus; feather boa kelp, Egregia; belt kelp, Laminaria; and palm kelp, Eisenia; are the main and preferred foods of red abalone, Haliotis rufescens Swainson; pink abalone, Haliotis corrugata Wood; white abalone, Haliotis sorenseni Bartsch; and green abalone, Haliotis fulgens Philippi (Cox 1962, Leighton 1966, Leighton 1968, Tutschulte and Connell 1988). Haliotis cracherodii Leach showed a preference for brown algae, M. pyrifera, E. menziesii, and Pelvetia fastigiata (J. Ag.) De Toni (Leighton and Boolootian 1963). Kelps commonly used as food for abalone in California mariculture are M. pyrifera and E. menziesii. The former is a valuable food for young red abalone, but a relatively poor diet for green abalone (Leighton 1989). Egregia is effectively used by both species and is the diet of choice for culture of green abalone (Leighton et al. 1981).

In contrast, red algae were found to be the main food items of two New Zealand species, *Haliotis iris* Gmelin and *Haliotis australis* Gmelin (Poore 1972). Australian abalone also apparently prefer to eat red algae but will consume some species of brown algae, generally when preferred species are uncommon (Shepherd and Steinberg 1992). For example, *Haliotis laevigata* Donovan rejects nearly all species of brown and green algae and prefers red algae and seagrass blades. *H. rubra* Leach feeds extensively on the fronds of the large "kelp," *Phyllospora*, on drifting blades of the giant kelp, *M. pyrifera*, and red algae, depending on the site. *Haliotis roei* Gray feeds preferentially on red algae, such as the short red algal "turf" seaweed, *Pterocladia* (Shepherd 1975).

Along the western coast of Baja California, Dawson et al. (1960). Guzmán del Próo et al. (1972, 1991), and Mateo-Cid and Mendoza-González (1994) have studied the associated flora in the natural habitats of the different abalone species in southern Baja California and found that the principal components of the abalone

habitat are brown algae, M. pyrifera, E. arborea, and other Laminariales; red algae, Gelidium, Acrosorium, and Plocamium; the articulated coralline algae, Bossiella and Corallina spp.; the crustose coralline algae, Lithothamnium and Lithophyllum; and the seagrass, Phyllospadix torreyi S. Watson. These species support the main gastropod grazers in the community including Tegula eiseni Jordan, Tegula aureotincta Forbes, Ocenebra foveolata Hinds, Haliotis spp., and Astraea undosa Wood (Guzmán del Próo et al. 1991).

Although it has sometimes been assumed by fishermen that Mexican abalone species feed extensively on *Macrocystis*, there have been no local studies on the natural diet or feeding habits of these species. Moreover, *Macrocystis* is not present in abalone banks around Punta San Roque (27°N lat) to Magdalena bay (24°N lat), the southern limit of the commercial abalone range, although as drift, *M. pyrifera* does occur as far south as Punta Abreojos (26°N lat). In Baja California, there are seven abalone species, but only five have commercial interest; *H. fulgens*, *H. corrugata*, *H. cracherodii*, *H. rufescens*, and *H. sorenseni*. Green abalone are the main resource of the Mexican abalone fishery.

The purpose of this article is to identify the food plants consumed by adult. *H. fulgens* through examination of gut contents of specimens collected along the southern part of its range, Baja California Sur, México, at sites largely beyond the current distribution range of *M. pyrifera*. We sought to determine the relative importance of brown and red algae as food for abalone living in that area. Studies on natural diets, growth on specific algal diets, digestive processes, digestibility, and conversion efficiency for algae by marine herbivores of commercial interest are important. A better understanding of these subjects will help suggest optimal diets for abalone culture.

MATERIALS AND METHODS

Green abalone were collected from four study sites along the coast of Baja California Sur-"Punta Prieta," 40 km south of Bahía Asunción; "La Piedra de la Orilla" at La Bocana; "Piedra de Afuera" at Punta Abreojos; and "La Punta, El Cora y Amarillo" at Las Barrancas-in August and September 1995 and March 1996 by personnel of Centro Regional de Investigaciones Pesqueras, CRIP-La Paz (Abalone project) and of the fishermen's cooperatives Leyes de Reforma, Progreso, Punta Abreojos, and Puerto Chale (Fig. 1). These sites are beyond the present distribution range of the brown alga M. pyrifera. This species of kelp is found from Alaska to Baja California, México (Abbott and Hollenberg 1976). Stands can occur as far south as Punta Asunción-Punta San Hipólito in Baja California, México (27°N lat; Dawson 1951), but this southern limit varies. At the time of sampling, the most southerly plants were around Punta San Roque, over 15 km northwest of Bahía Asunción (Serviere pers. obs.).

The specimens were collected by Hookah divers. All diving was done in the early morning. Four or 5 h after collection, the specimens were delivered to the shore, and the sex and shell length of each abalone sampled were recorded. The digestive tracts of 30 specimens from each site were donated by the cooperatives for the study (Table 1). Guts were labeled and preserved in 10% formalin in seawater neutralized with sodium borate.

In the laboratory, each digestive tract was dissected and the crop and stomach contents were washed with distilled water, recovered on a 1-mm-pore-size mesh sieve, and weighed while wet (McLean 1970). The different groups present were separated by

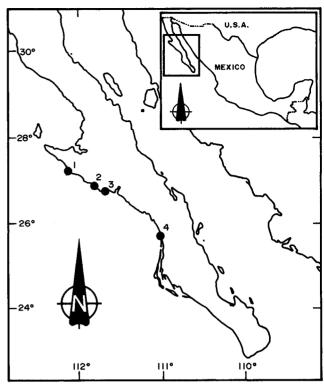


Figure 1. The study sites: 1, "Punta Prieta," 40 km south of Bahía Asunción; 2, "La Piedra de la Orilla," La Bocana; 3, "Piedra de Afuera," Punta Abreojos; 4, "La Punta, El Cora y Amarillo," Las Barrancas.

viewing with a stereoscopic microscope and identified to the lowest taxonomic level permitted by the degree of digestion of the contents. It was necessary to compare algal fragments in detail (external, internal, and reproductive morphology) with macroalgae collected from the benthic community at nearby sites or with herbarium specimens. The keys and species descriptions of Abbott and Hollenberg (1976), Dawson (1953, 1954, 1963), Hollenberg and Dawson (1961), Phillips and Meñez (1988), and Taylor (1960) were used to guide our identifications.

The frequency for each species was calculated from the number of guts in which the species occurred among the total number of guts sampled, and the relative frequency was calculated from

Relative frequency =
$$\frac{\text{number of occurrences}}{\text{number of guts}} \times 100$$

Relative frequency was obtained for each site and also for the total guts analyzed.

Differences in mean shell length, weight of gut contents, and number of species per gut between study sites were analyzed with the nonparametric Kruskal-Wallis test (Sokal and Rohlf 1995). Multiple comparison procedures (Kolmogorov-Smirnov test) were used to test for significant differences between means. All statistical procedures were done with the program STATISTICA 5.0 for PC.

RESULTS

The range in shell length for the abalone studied was 71.0–182.0 mm, and the overall mean \pm SD was 134.04 ± 22.09 mm. The mean size was significantly different between sites (Kruskal-

TABLE 1.							
Location, shell length,	and sex of the green	abalone analyzed.					

Sites	Geographic Location	Date	n*	Shell Length (mm)†	Sex‡
Bahía Asunción, "Punta Prieta"	114°17′40″ W 27°07′00″ N	Sept. 4, 1995	30	141.04 ± 15.08	11♂, 11♀ 8?
La Bocana, "La Piedra de la Orilla"	113°41′35″ W 26°46′30″ N	, Sept. 2, 1995	29	143.96 ± 28.26	13♂, 10♀ 6?
Punta Abreojos, "Piedra de Afuera"	113°34′05″ W 26°41′50″ N	Aug. 31, 1995	31	129.30 ± 21.58	15♂, 12♀ 4?
Las Barrancas, "La Punta, El Cora y Amarillo"	112°27′00″ W 26°14′00″ N	March 8, 1996	30	120.40 ± 10.01	9♂,6♀ 15?

^{*} n, Sample size of abalone examined.

Wallis test, H=25.54; p < 0.0001). The mean size of abalone from banks at the northern sites, Bahía Asunción (141.04 ± 15.08, mean ± SD) and La Bocana (143.96 ± 28.26), was greater than the size of abalone found at the southern sites, Punta Abreojos (129.30 ± 21.58) and Las Barrancas (120.40 ± 10.01) (Kolmogorov-Smirnov test, p < 0.05).

The consistency and wet weight of gut contents among individuals were different, depending in part on the degree of digestion and the time since last feeding in each (Fig. 2). In general, the contents were fragments of macroalgae and seagrass larger than 1 mm. However, in some individuals, the stomach contents were more liquid, probably because digestion was more advanced, and in these, there were few fragments of macroalgae and seagrass larger than 1 mm. The average wet weight (grams \pm SD) was 1.05 \pm 0.73 at Bahía Asunción, 3.57 \pm 2.23 at La Bocana, 1.99 \pm 1.57 at Punta Abreojos, and 3.59 \pm 2.6 at Las Barrancas. Differences between the content weights for abalone from the different sites were tested (Kruskall Wallis test, H = 21.85; p < 0.0001).

The smallest number of species per individual gut was one, and the largest was six (Fig. 3). The average number of plant species per gut was similar at three sites: Bahía Asunción $(3 \pm 1, \text{ mean } \pm \text{SD})$, La Bocana (2 ± 1) , and Punta Abreojos (2 ± 1) . The highest average was at Las Barrancas (4 ± 1) and was significantly different (Kolmogorov-Smirnov test, p < 0.01).

The components found in the crop and stomach contents of 121 green abalone adults were 12 species, of which 4 were Phaeophyta,

7 were Rhodophyta, and 1 species was seagrass (Table 2). The number of species in all guts at Las Barrancas was nine, followed by Bahía Asunción (n=8), La Bocana (n=7), and Punta Abreojos (n=5). In general, the species diversity of red algae predominated over brown algae. In Punta Abreojos specimens, however, red and brown algae were equally represented.

Guzmán del Próo et al. (1991) studied the associated flora of the abalone species in Bahía Tortugas (27°N lat) and reported 4 species of Chlorophyta, 11 species of Phaeophyta, 29 species of Rhodophyta, and 1 spermatophyta. The number of species in summer was 22, and in winter, it was 27. Mateo-Cid and Mendoza-González (1994) found 113 species of benthic marine algae at Bahía Asunción (27°N lat): 3 species of Cyanophyta, 13 species of Chlorophyta, 19 species of Phaeophyta, and 78 species of Rhodophyta. The greatest diversity occurred in summer with 110 taxa; 40 species were found in winter. At Bahía Magdalena (24°N lat), a total of 132 species were identified-22 species of Chlorophyta, 22 species of Phaeophyta, and 88 species of Rhodophyta. The greatest diversity occurred in winter, with 77 species; 66 species were found in summer (Sánchez-Rodrígez et al. 1989). M. pyrifera, E. arborea, Corallina officinalis L., Corallina pinnatifolia (Manza) Daws., and P. torreyi were the principal components of the benthic vegetation of Bahía Tortugas and Bahía Asunción. Codium magnum Daws., Caulerpa sertularioides (S.G. Gmel.) Howe, Colpomenia tuberculata Saund., E. arborea, Sargassum sinicola S. & G., Padina durvillaei Bory, Hydroclathrus clathratus

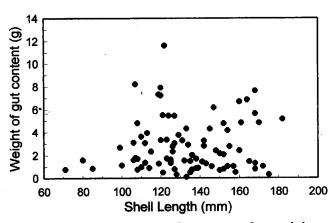


Figure 2. Shell length and weight of gut contents of green abalone.

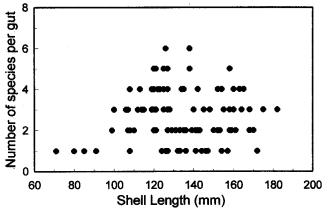


Figure 3. Shell length and number of species per gut of green abalone.

[†] Mean ± SD.

^{‡ ♂,} male; ♀, female; ?, not identified.

TABLE 2.

List and relative frequency of species identified in the crop and stomach contents of green abalone.

Species	Sites*				
	Bahía Asunción	La Bocana	Punta Abreojos	Las Barrancas	All Sites*
Phaeophyta					
Eisenia arborea Aresh.	14	22		22	16
Padina sp.	1			1	1
Sargassum sp.	23	19	52		19
Spatoglossum sp.	S.e.		2		1
Rhodophyta					
Cryptopleura crispa Kylin	13	26	12	16	16
Gelidium robustum (Gardn.)	10	5			4
Hollenb. & Abb.					
Erythrotrichia sp.	,			4	1
Polysiphonia sp.				11	4
Prionitis sp.	1	1		. 1	1
Rhodymenia sp.	4	17	18	16	13
Red NI†				12	4
Seagrass					
Phyllospadix torreyi S.	32	10	16	17	19
Watson					
Total species	8	7	5	9	12

^{*} Relative frequency.

(C. Ag.) Howe, Corallina spp., Amphiroa magdalenensis Daws., Amphiroa zonata Yendo, Laurencia pacifica Kylin, Pterocladiella capillacea (S.G. Gmel.) Santelices and Hommersand, and Spyridia filamentosa (Wulf.) Harv. were most common at Bahía Magdalena.

Five species had the greatest relative frequency and made up most of abalone diets at the sites studied along Baja California Sur. *P. torreyi* had the highest value, followed by the brown algae *Sargassum* sp. and *E. arborea* and the red algae *Cryptopleura crispa* and *Rhodymenia* sp. The value of each was different at different sites (Table 2). The brown algae *Sargassum* and *Eisenia* and the red algae *Cryptopleura* and *Rhodymenia* made up about 50% of the recovered food items at Bahía Asunción (brown, 37%; red, 13%) and Las Barrancas (brown, 22%; red, 32%) and about 80% at La Bocana (brown, 41%; red, 43%) and Punta Abreojos (brown, 52%; red, 30%) and averaged about 60% over all sites (brown, 35%; red, 29%). *P. torreyi* was present in 32% of guts at Bahía Asunción and about 15% in the other localities and averaged about 15% over all sites. No other plant occurred in more than 12% of the guts of the green abalone examined.

DISCUSSION

The analysis of shell length of abalone from Bahía Asunción, La Bocana, Punta Abreojos, and Las Barrancas suggests that the mean size of green abalone decreases from north to south. The shell length (in millimeters) of abalone at Bahía Asunción (141.04 \pm 15.08, mean \pm SD) was larger than that at Las Barrancas (120.40 \pm 10.01). Guzmán del Próo et al. (1976) observed the size and weight means for *Haliotis* spp. to decrease from north to south, following a gradient along the peninsula. Data for samples from the commercial catch showed the same trend for the maximum length of *H. corrugata* and *H. fulgens* (Vega-Velazquez et al. 1994).

The range of gut content weights for individuals of the same

size was wide. For example, at the shell length of 130 mm, values from 0.12 to 4.33 g were measured. The differences between individuals of the same or different populations appear related more to the progression of digestion in each individual rather than its size, because the weight of gut content was from the fragments of macroalgae and seagrass larger than 1 mm, and not for the liquid stomach content. The progress of digestion in the organisms sampled is relative to the time that the abalone began or stopped feeding and with the time of collection of abalone. The digestive tracts were preserved 4 or 5 h after the time of collection, and the content weight then consists of fragments not immediately digested. Nevertheless, no abalone with an entirely empty crop and stomach were found in the samples, and in general, in the contents, we always found fragments of macroalgae and seagrass larger than 1 mm. Faole and Day (1992), in laboratory assays, found that when abalone are well fed, they eat only the preferred species and process these rapidly, but when food is scarce, they are less selective and process the food slowly. Therefore, one must be cautious in assessing diet based only on gut contents.

The average number of species per individual gut was 2 ± 1 (mean \pm SD), except at Las Barrancas (4 ± 1). Abalone from three similar sites were collected during summer and, at Las Barrancas, during winter. The season of the sampling is important because it has been suggested that the diets reflect the species most abundant in the habitat at the time of sampling, and the relative abundance of food item in the diet may be related to its availability in the environment. Southern sites on the peninsula of Baja California have the greatest floral diversity in winter. Sánchez-Rodrígez et al. (1989) identified 77 species in winter and 66 species in summer. Poore (1972) found seasonable variation in the diet composition of a New Zealand species, *H. iris*, and Barkai and Griffiths (1986) describe the diet of a South African abalone *Haliotis midae* at two sites being more diverse in winter than in summer. However, site

[†] Red NI, red algae not identified.

appears to be a more important variable than season. It is necessary to extend this preliminary survey with detailed field studies on the natural diets of Mexican abalone species with quantitative analysis of local flora to determine the relation between availability of food and principal food to abalone. Feeding experiments are needed to determine preference and utilization.

Although along the Pacific Coast of Baja California Sur, the benthic environments inhabited by abalone are characterized by a flora with more than 50 species (Guzmán del Próo et al. 1991, Mateo-Cid and Mendoza-Gonzalez 1994, Sánchez-Rodrígez et al. 1989), only seven red algae, four brown algae, and one seagrass were identified from gut content analysis of green abalone. Of these, Macrocystis, and Eisenia have been reported as algal foods of H. fulgens in southern California (Leighton 1966, Tutschulte and Connell 1988). Gelidium robustum, E. arborea, and P. torrevi have been concluded to be important species in abalone communities and potential abalone food along Baja California (Guzmán del Próo et al. 1972, Guzmán del Próo et al. 1991). The red algae C. crispa, Erythrotrichia sp., Polysiphonia sp., and Prionitis sp. and the brown algae Padina sp., Sargassum sp., and Spatoglossum sp. had not been previously reported as algal food of green abalone.

Guzmán del Próo et al. (1972, 1991) suggested that species such as articulated corallines *Bossiella* and *Corallina* spp. and crustose corallines *Lithothamnium* and *Lithophyllum* are important elements that form part of the habitat of abalone species in Baja California, as well as all over the world, and are related to postlarval diet. Although corallines and crustose algae are found in the local flora of the sites studied (Abbott and Hollenberg 1976, Dawson 1953), we did not observe them in the gut contents. These species and their epiphytes are used by small abalone.

The relative frequency of species at the four sites suggests that although green abalone in Baja California Sur accept a wide range of macrophytes, the principal conspicuous elements in the ingesta were the seagrass *P. torreyi* and the macroalgae *Sargassum* sp. (Fucales), *E. arborea* (Laminariales), *C. crispa* (Ceramiales), and *Rhodymenia* sp. (Rhodymeniales). The other species found in abalone guts could be considered species that are eaten incidentally with the main food according to the local flora. Poore (1972) studied the diets of a single species (*H. iris*) from two widely differing locations and concluded that the floral composition has a major effect on the abalone diet, which varies markedly from place to place, even within a small geographical area. Similarly, Leighton and Boolootian (1963), from study of gut contents of *H. cracherodii*, a common littoral inhabitant of rocky southern California

and Baja California shore lines, found that the contents largely reflected the flora of the local intertidal zones.

Our results show that for green abalone along Baja California Sur, both brown algae (*Sargassum* and *Eisenia*) and red algae (*Cryptopleura* and *Rhodymenia*) have importance as food plants. These species occurred in about 50% of the content samples from Punta Prieta and Las Barrancas and about 80% at La Bocana and Punta Abreojos and averaged 60% at all sites. Cox (1962) and Shepherd and Steinberg (1992) mentioned that brown algae predominate in the diet of green abalone. Leighton (1966) conducted feeding experiments that demonstrated that green abalone had a distinct preference for brown algae, in particular, *Macrocystis* and *Egregia*. The second species is the diet of choice for culture of green abalone (Leighton et al. 1981, Leighton 1989). The only red alga tested in Leighton's 1966 study, *Gigartina armata*, had a relatively low preference value.

The diet an abalone consumes in the field must be seen as a compromise between the need to consume a balanced diet and such factors as food availability, avoidance of algae with chemical deterrents, and an inability to consume tough food (Fleming 1995). Where feeding studies have been done with captive green abalone, algae like Padina and Sargassum were little ingested and had relatively limited food value. The same is true of the red alga Pterocladia and the surf grasses Phyllospadix spp. (Leighton pers. comm.) This study suggests that controlled feeding and growth experiments and in vitro digestibility tests should be conducted wherein the algae found in abalone gut content samples may be appropriately evaluated for their nutritive value. It may be that H. fulgens in the southern part of its range has adapted enzymatically and may use some of these algae more effectively than in northern populations (Serviere-Zaragoza et al. 1997). Eisenia is a fairly good food, and where it predominates in drift or among rocks and is available to the abalone, it will support growth.

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