'FIERY BODIES' - ARE PYROSOMAS AN IMPORTANT COMPONENT OF THE DIET OF LEATHERBACK TURTLES?

JOHN DAVENPORT 1,3 and GEORGE H. BALAZS 2

¹ School of Ocean Sciences, University of Wales at Bangor, Marine Science Laboratories, Menai Bridge, Gwynedd LL59 5EY, U.K.

² National Marine Fisheries Service, Science Southwest Fisheries Center, Honolulu Laboratory, 2570 Dole St., Honolulu, Hawaii 96822-2396, U.S.A.

³ Present address: University Marine Biological Station, Millport, Isle of Cumbrae, Scotland, KA28 0EG, U.K.

INTRODUCTION

Until the careful work of Bleakney (1965) and Brongersma (1969) the diet of Leatherback Turtles (Dermochelys coriacea (L.)) was obscure; they were variously thought to be herbivores, omnivores, predators on fish or crustacea, or specialist squid-eaters. Bleakney and Brongersma (op. cit.) established from analysis of stomach contents that the diet of Leatherbacks caught or stranded in coastal waters of North America and Europe was made up of jellyfish (medusae) and associated animals (such as hyperiid amphipods). Direct observations of jellyfish-eating have since been made, particularly around the Irish, Welsh and French coasts, where Leatherbacks are regularly observed consuming large medusae in August and September. The concept that Leatherbacks are specialized medusivores has been widely accepted, and Holland et al (1990) recently demonstrated that the fatty acid signature of Dermochelys blubber is compatible with a jellyfish diet. However, in this paper we demonstrate that another group of animals, the pyrosomas ('fiery bodies' so named by virtue of their bright bioluminescence) may also be important dietary items in some circumstances.

Three major groups of gelatinous, pelagic marine animals are known; the cnidarians (medusae and siphonophores), the ctenophores (combjellies) and the tunicates. As far as Leatherback diet is concerned, most observers have concentrated upon the carnivorous cnidarians, particularly the swarms of jellyfish which are seen in temperate and tropical coastal waters, and on which Dermochelys is known to feed. However, in the waters above the continental slope, and in the open ocean, tunicates (which are predominantly herbivorous) are at least as common. Two groups of tunicates, the pyrosomas and the salps, attain sizes great enough to make them potential prey for adult Leatherbacks; they also occur in dense swarms in areas of upwelling where primary production is high.

Pyrosomas are colonies of tunicate zooids embedded in the walls of gelatinous tubes which are closed at one end and open at the other (Berrill, 1950). Each zooid draws water individually from the surrounding sea (through the branchial siphon), but all zooids exhale through the atrial siphons into the interior of the tube, thereby producing jet propulsion via its open end (guarded by a diaphragm). This propulsion is powerful enough to permit extensive vertical migrations. During the day pyrosomas are often found at depths of 500-800 m (within the known diving capability of Leatherbacks – Eckert et al, 1986), but migrate upwards at night, often into surface waters (Marshall, 1979). Pyrosomas are brightly luminescent, producing bluegreen light (482m) with a secondary green peak (525m) according to Boden and Kampa (1964). Pyrosoma light displays last for many seconds, even minutes. Pyrosomas range in size from a few cm to more than 4 m according to Marshall. Specimens 0.2-0.5 m are very common in summer. They can be soft in texture, but most of the larger pyrosomas are rather cartilagenous/leathery despite their gelatinous nature.

Salps are barrel-shaped tunicates. Some are solitary and can be up to 0.2 m in length; others occur in chain-like colonies (up to 2 m length), whose jet propulsion (muscular in this case) is synchronized. Like pyrosomas, salps are bioluminescent and distributed widely through the top 800 m of the water column. Salps have a very high water content (98.3% according to

Riley and Gorgy, 1948), which would superficially make them rather meagre food resources. However, Kashkina (1986) notes that salps (and by implication other tunicates including pyrosomas, since all share a common feeding mechanism) have a stomach (the 'nucleus') full of compacted phytoplankton, detritus and microzooplankton. He also lists a wide variety of fish which feed upon salps and pyrosomas, often as major items of diet. Fish living in upwelling areas, near sea mounts and on the continental slope, seem particularly dependent upon pelagic tunicates.

Davenport (1988) suggested that the Leatherback might forage upon pyrosomas during deep dives; he thought that the colonies might be located by their bioluminescence. Direct evidence to support this hypothesis was lacking, although Marshall (1979) stated that sea turtles (species unspecified), together with sea birds and fish, had been observed to feed on glowing pelagic tunicates at the sea surface at night.

This paper lists records of occurence of pyrosomas in the gut of Leatherback Turtles and also presents details of the food value of pyrosomas, including an analysis of their fatty acid composition.

ANALYTICAL METHODS

Large numbers of *Pyrosoma atlantica* were collected on Cruise 195 of R.V. *Discovery* off the west African coast. Collection, by midwater net (8 m² mouth), took place in September 1990 in a large sea area (roughly 17-21 N; 19-25 W) at depths between 500 and 1000m. The colonies were washed briefly in fresh water, dried in absorbant paper, placed in polythene bags and frozen at -20°C. On return to a shore facility four colonies were analyzed in the following manner. The colonies were each weighed, dried in a freeze-drier and reweighed. Duplicate pieces of dried material were taken from each colony, weighed, ashed in a furnace at 570°C, allowed to cool in a desiccator and reweighed. Other samples of dried material were analyzed for protein content by a micro-Kjeldahl technique, for caloric content by wet oxidation (using an appropriate correction for unreacted protein) and for lipid content by solvent extraction and subsequent gravimetric measurement. Samples of pyrosoma lipid were further analyzed for fatty acid composition by gas chromatography.

RESULTS

- 1. RECORDS OF LEATHERBACKS FORAGING ON *PYROSOMA* IN THE INSULAR NORTH PACIFIC OCEAN
- a) Iverson & Yoshida (1956) plus personal communication to G. Balazs by Tom Hida.

Date and Location: May 21st, 1954, 5 57.5' N, 161 11.0' W; on the high seas, 100 km east of Palmyra Island.

A Leatherback of greater than or equal to 91 cm carapace length was tangled in longline fishing gear. The "gastrointestinal tract found to be filled completely through with Pyrosoma".

b) by Jones & Shomura (1970).

Date and Location: July 21st, 1969. 3 30' N, 145 0' W; on the high seas.

106 cm carapace length Leatherback hooked alive in the "shoulder" in longline fishing gear. Report states "stomach contents of the Leatherback turtle were examined and consisted entirely of *Pyrosoma* colonies".

c) Balazs & Gilmartin (unpublished data)

Date and Location: March 24th, 1982. 21 10' N, 157 43' W; Waimanalo Bay, Oahu, Hawaiian Islands.

137 cm carapace length Leatherback stranded ashore alive, with all four flippers recently amputated, presumably by sharks. "When necropsied, the gastrointestinal contents were found to consist of liquid, one whole *Pyrosoma* and several *Pyrosoma* fragments, and three pieces of cellophane".

From these records it seems that pyrosomas are found in the gut of turtles foraging in oceanic waters (rather than on the continental shelf). Pyrosomas may also be identifiable throughout the gut (Iverson & Yoshida, 1956).

2. RECORDS OF LEATHERBACKS FORAGING ON *PYROSOMA* IN THE SOUTH PACIFIC OCEAN

Some years ago one of the authors (JD) saw a mounted Leatherback in the Dunedin Museum, South Island, New Zealand. The associated label stated that the turtle had been caught in oceanic waters north of North Island, New Zealand; it had pyrosomas in the stomach.

3. RECORDS OF LEATHERBACKS FORAGING ON PYROSOMA IN THE MEDITERRANEAN

Location: Gulf of Genoa, northern Mediterranean.

Capra (1949) found "remains of six specimens of a *Pyrosoma* species in the intestine of a Leathery Turtle, which had become entangled in nets off the Punta della Chiappa. One *Pyrosoma* specimen had a length of 50 cm, but it was much lacerated; the others measured 15 to 20 cm".

4. ANALYSIS OF PYROSOMA ATLANTICA TABLE 1 Water and organic content of Pyrosoma atlantica

Colony no.	Wet wt (g)	dry wt (g)	dry wt as % wet wt	water as %wet wt
1	52.57	2.87	5.46	94.54
2	46.92	2.27	4.84 95.16	
3	21.33	1.57	7.36 92.64	
4	16.49	1.25	7.58	92.42
		mean	6.31	93.69
		SD	1.37	1.37
Colony no.	Ash as % dry wt		Organic content as % dry wt	Organic content as % wet wt
1	65.7		34.3	
1	67.5		32.5	1.82
2	62.4		37.6	1.80
2	63.4		36.6	1,00
3	60.4		39.6	2.02
3	57.4		42.6	3.02
4	55.3		44.7	
4 54.7		45.3	3.41	
mean	60.8		39.2	2.51
SD	4.7		4.7	0.83

Table 1 shows the water and organic content of *Pyrosoma atlantica*. The tunicate colonies have a water content of about 94%; some 39% of the dried material is organic in nature, 61% inorganic. In consequence, only 2.5% of the weight of live colonies is composed or organic material. The water contents are similar to those of cnidarians (medusae and siphonophores) (Marshall, 1979), but pyrosomas are less watery than salps. The organic content of pyrosomas is close to the upper limit of the range (0.5-2.5%) given for medusae by Teissier (1926).

TABLE 2
Biochemical composition of Pyrosoma atlantica

Colony no.	mean protein content (g protein/mg dry wt)	mean lipid content (g lipid/mg dry wt)	mean calorific content (cals/mg dry wt)	
1	90.6	9.0	0.78	
2	110.4	-	1.04	
3	91.3	14.0	1.26	
4	134.4	-	1.66	
mean	106.7	11.5	1.18	

Table 2 shows the biochemical makeup of dried *Pyrosoma*. Taken with the organic content data shown in Table 1, this means that about 27% of the organic material in pyrosomas is composed of protein, 3% of lipid and (by difference) 70% of carbohydrate (presumably mainly mucopolysaccharides to give the gelatinous structure). Both protein and lipid values are low by the standards of marine animals such as fish and mollluscs which might be expected to have protein and lipid contents of about 45% and 8% respectively). However, the values are not dissimilar from those reported from cnidarians. The caloric value (about 3 cals/mg dry organic wt) is also very low, lower than all of the organisms listed by Crisp (1971).

Fatty acid composition (%) of two colonies of *Pyrosoma atlantica*. Data for Leatherback turtle carapace blubber (neutral fraction) and for jellyfish (*Rhizostoma*, *Cyanea*) are given for comparison; they are taken from Holland, Davenport & East (1990)

Fatty	acid	Pyros Colo 1	soma ony no. 2	Dermochelys	Rhizostoma	Cyanea
A. Sa	turated					
12:0 13:0 14:0 15:0 16:0 17:0 18:0 19:0		14.8 36.5 3.3	12.5 25.9 1.9	5.6 tr 11.5 0.6 15.9 0.8 7.5 0.3	0.3 0.6 5,1 2.0 27.3 2.3 21.7 0.5	0.1 0.3 3.5 1.3 19.0 1.0 12.0
20:0	onounsatura	ted -	-	0.3	tr	1.8
16:1 16:1 18:1 18:1 20:1 22:1	7 9 9 7 9	6.1 10.1 1.6 - 2.8	5.9 12.2 2.2 0.4 1.3	9.5 - 25.4 4,9 2.2	3.8 6.8 3.5 0.8	4.7 5.5 3,1 3.4 2.5
C. Pol 18:2 18:3 18:4 20:8 20:5 22:5 22:6	lyunsaturate 6 3 3 6 3 6	1.9 1.3 2.3 2.3 4.2 1.2	3.2 1.2 3.1 3.5 5.9 0.7 20.3	1.5 0.6 0.4 2.1 4.5 1.8 4.6	1.6 1.6 2.8 2.8 9.7 1.3 5.3	0.4 0.4 0.6 8.7 13.8 3.2 12.1

tr = trace quantities; - = not detected

Table 3 shows the fatty acid composition of *Pyrosoma*. As with jellyfish, pyrosoma lipids are rich in the saturated fatty acids 14:0 and 16:0, the monounsaturated fatty acid 18:1 9 and the polyunsaturated fatty acids 20:5 3 and 22:6 6. There are also reasonable levels of arachidonic acid (20:4 6). These data, combined with those for Leatherback blubber (Holand et al, 1990) are consistent with the concept of a phytoplankton – pyrosomas – Leatherback food chain (assuming that Leatherbacks accumulate fatty acids directly from the diet, rather than synthesizing them de novo).

DISCUSSION

The records drawn together here, plus the results of the analysis of *Pyrosoma atlantica* indicate that pyrosomas are important items of the Leatherback diet and have a composition quite similar to medusae. It is tempting to speculate that pyrosomas are more important to Leatherbacks swimming in mid ocean than they are to turtles foraging in coastal water, but more data are needed to clarify this point, particularly as Capra (1949) reported pyrosomas from the gut of a turtle swimming in the relatively shallow Gulf of Genoa. As Den Hartog & Van Nierop (1984) point out, the whole concept of medusivory stems from analysis of stomach contents of a relatively small number of Leatherbacks stranded or observed in northern temperate waters. Given that Leatherbacks are also known to eat the Portuguese Man O'War (a siphonophore – *Physalia*) (Bacon, 1970) and inappropriate floating objects such as plastic bags and polystyrene, it seems likely that *Dermochelys* is an opportunist rather than a specialist predator on fairly large, slow moving gelatinous prey.

A longstanding problem in considerations of the nutrition of Leatherbacks is that their food is very watery and the organic component is made up largely of mucopolysaccharides. This is true whether the diet is predominantly of medusae (the conventional view) or is made up to some extent of tunicates (this paper). Such a poor quality diet means that adult Leatherbacks must consume very large quantities of food (perhaps 20-30% body weight per day, rather than the 3-5% of Green and Loggerhead turtles). Duron (1978) reported that large Leatherbacks foraging on the medusa Rhizostoma off the French coast each ate about 200 kg of jellyfish per day. However, there are still problems in assimilating protein and lipids from jellyfish or tunicates, against a background of essentially indigestible mucopolysaccharide. Kashkina (1986) has raised an interesting possibility; that salp-eating fish probably only assimilate energyrich material from the salp stomach, and pass the bulk of the gelatinous tunic through the gut without digesting it. This reasoning could equally be applied to medusae, which will contain partly digested food within the stomach and radial canals, and also have concentrations of organic material in the gonads during the breeding season. If a Leatherback turtle could gain access to the more 'valuable' parts of prey, it would not need to waste time and energy in digesting the tunic of tunicates and the mesogloea of coelenterates. Leatherback turtles cannot chew food items, which appear to be swallowed whole, or at least in large chunks. However, the entire oesophagus of Dermochelys, which may be more than 2 m long in large specimens, is lined with hundreds of long, semirigid cornified conical processes; the oesophagus is also very muscular, probably allowing the oesophageal contents to be squeezed by peristaltic waves. If cnidarians and salps were effectively shredded, the tubular conformation of pyrosoma colonies presents a relatively large surface area to the surrounding medium. At least one of the records presented here (Iverson & Hoshida, 1956; Hida, pers. comm.) indicates that some pyrosomas are still identifiable in the hind gut - supporting the idea of the tough test passing through the digestive tract relatively unchanged.

ACKNOWLEDGEMENTS

J.D. wishes to thank Dr. Peter Herring for inviting him to take part in Cruise 195 of RV Discovery, and the University of Wales at Bangor for providing travel funding. He also wishes to thank Mr. J. East for carrying out biochemical analyses. G.B. thanks Tom Hida and Mike Seki for information and helpful discussions regarding pyrosomas.

REFERENCES

Bacon, P.R. (1970). Studies on the leatherback turtle *Dermochelys coriacea* (L.), in Trinidad, West Indies. *Biological Conservation*, 2, 213-217.

Balazs, G.H. & Gilmartin, W.G. Unpublished data.

Berrill, J.J. (1950). The Tuniccata, The Royal Society: London.

Boden, B.P. & Kampa, E.M. (1964). Planktonic bioluminescence. Oceanography and Marine Biology Annual Review, 2, 341-371.

Bleakney, J.S. (1965). Reports of marine turtles from New England and eastern Canada. Canadian Field Naturalist, 19(2), 120-128.

Brongersma, L.D. (1969). Miscellaneous notes on turtles, IIB. Proceedings of the Koninklijke Nederlanse Akademie Van Wetenschappen Series C, 72, 90-102.

- Capra, F. (1949). La Dermochelys coriacea (L.) nel Golfo di Genovo e nel Mediterraneo (Testdu. Sphargidae). Ann. Mus. Civ. Stor. Nat. Genovo, 63, 270-282.
- Crisp, D.J. (1971). Energy flow measurements. In *IBP Handbook No. 16. Methods for the Study of Marine Benthos* (ed. N.A. Holme & A.D. McIntyre). Blackwell: Oxford.
- Davenport, J. (1988). Do diving leatherbacks pursue glowing jelly? British Herpetological Society Bulletin, 24, 20-21.
- Den Hartog, J.C. & Van Nierop, M.M. (1984). A study on the gut contnets of six leathery turtles *Dermochelys coriacea* (Linnaeus) (Reptilia: Testudines: Dermochelyidae) from British waters and from the Netherlands. *Zoologische Verhanelingen Leiden*, 20, 1-36.
- Duron, M. (1978). Contribution à l'étude de la biologie de *Dermochelys coriacea* (Linné) dans les Pertuis Charentais. *Thèse Universite Bordeaux 3me cycle*. 1465.
- Eckert, S.A., Nellis, D.W., Eckert, K.L. & Kooyman, G.L., 1986. Diving patterns of two leatherback sea turtles (*Dermochelys coriacea*) during interesting intervals at Sandy Point, St. Croix, U.S. Virgin Islands. *Herpetologica*, 42(3), 381-388.
- Holland, D.L., Davenport, J. & East, J. (1990). The fatty acid composition of the leatherback turtle Dermochelys coriacea and its jellyfish prey. Journal of the Marine Biological Association of the United Kingdom, 70, 761-770.
- Iverson, E.S. & Yoshida, H.O. (1956). Longline fishing for tuna in the Central Equatorial Pacific, 1954. U.S. Fish and Wildlife Service, Special Scientific Report Fisheries No. 184 33p.
- Jones, E.C. & Shomura, R.S. (1070). Narrative report Townsend Cromwell, Cruise 44. Bureau of Commercial Fisheries, Biological Laboratory, Honolulu. Unpublished report, 1 pp.
- Kashkina, A.A. (1986). Feeding on fishes of salps (Tunicata, Thalliacea). Voprosy Ikhtiologii, 3, 440-447.
- Marshall, N.B. (1979). Developments in Deep Sea biology, Blandford Press: Poole, Dorset, U.K.
- Riley, G.A. & Gorgy, S. (1948). Quantitative studies of summer plankton populations of the Western North Atlantic. *Journal of Marine Research*, 7(2), 100-118.
- Teissier, G. (1926). Sur la teneur en eau et en substances de Chrysaora hyoscella (L.) aux différents stades sont ontogénèse. Bulletin Societe Zoologique Français, 51, 266-273.