353

Comparative role of salps and other zooplankton in the cycling and transport of selected elements and natural radionuclides in Mediterranean waters

S. KRISHNASWAMI[1], M. BASKARAN[1], S.W. FOWLER[2] and M. HEYRAUD[2]

[1] Physical Research Laboratory, Ahmedabad 380009, India
[2] International Laboratory of Marine Radioactivity, IAEA, Musee Oceanographique, MC 98000, Monaco

Abstract. Salps, salp fecal pellets and other zooplankton species were analyzed for a suite of elements and natural radionuclides to assess their role in the biogeochemical cycling of nuclides in oceanic waters. The nuclide/Al ratios in organisms normalized to the same ratio in crustal rock indicated that Ca, Sr, Zn, Cu, U, ^{210}Po, and ^{210}Pb are enriched in the organisms. The concentrations of Fe, Al, Th isotopes and ^{210}Pb in salps and fecal pellets were about an order of magnitude higher than those in salps, whereas Ca, Cu, Zn, Mn and Po were higher by factors of about 2–5. Fluxes via salp defecation were higher than those which have been measured in crustacean zooplankton species, a result primarily due to the high defecation rates characteristic of salps. High nuclide levels in salp fecal pellets coupled with high defecation rates and presumed high salp biomass in many areas underscore the importance of these indiscriminate filter feeders in packaging and transporting to depth particulate-associated nuclides in surface waters.

Introduction

The importance of marine organisms, particularly plankton, in controlling the distribution and cycling of elements and radionuclides in the oceans is well recognized (Lowman et al., 1971; Martin and Knauer, 1973; Fowler, 1977; Higgo et al., 1980; Bruland, 1983; Collier and Edmond, 1984). Much of the driving force in elemental cycling by plankton comes from a steady production of biogenic debris (fecal pellets, molts, phytoplankton hard parts, carcasses, etc.) in the upper water layers. In fact recent direct measurements of the settling fluxes of particulate matter and its components at various depths in the oceans indicate that fluctuations in these fluxes are controlled by variation in primary productivity in the euphotic zone (Deuser et al., 1981, 1983). Gelatinous zooplankton such as salps commonly constitute a major part of the plankton in oceanic and coastal waters during various times of the year (Alldredge and Madin, 1982). Despite their importance in terms of biomass the role of these organisms in the cycling and removal of trace elements and radionuclides from the water column is only poorly understood. With a veiw to obtain more information on gelatinous species, we collected several samples of salps and a sample of salp feces and analysed them along with some other zooplankton species for elemental and radiochemical composition.

Methods

During April—May 1984 salps and mixed zooplankton were collected approximately 3 km off Monaco using various mesh-size plankton nets. Most of the salp samples were the chain form of the species *Thalia democratica*, however, one sample was composed of *Salpa maxima*. Both salp species are common in northwestern Mediterranean waters, and particularly during the spring months often represent a large fraction of the zooplankton biomass in the upper 50 m (Braconnot, 1971). Salps were held live in ambient seawater and upon return to the laboratory were rinsed repeatedly with de-ionized doubly distilled water over a 2 mm nylon sieve and dried at 60°C for 3—4 days. Seasalt was abundant in some of the dried salp samples. These samples were rinsed with double distilled water and redried prior to chemical analysis. Samples for chemical analyses were made up of whole animals and were about 1 g dry weight. From one of the collections of *Thalia democractica* (16—4—84) live individuals were held for approximately 8 hr in a specially-designed fecal pellet collection device (La Rosa, 1976; Small et al., 1979) to obtain relatively large amounts of pure salp feces. This sample was briefly rinsed with double distilled water to remove adhering sea salt and also dried at 60°C.

In addition to salps, several samples of zooplankton were collected and prepared for analysis in the same manner as the salps. The samples consisted of the neustonic copepod *Anomalocera patersoni*, crab larvae (nearly pure) and mixed copepods (600—2000 μm size fraction). The problems of contamination inherent in collecting zooplankton for trace metal analyses are well documented (Martin and Knauer, 1973; Fowler, in press). Extreme care was taken to avoid metal contamination during all phases of shipboard collection and sample preparation. Pre-cleaned sample containers were used on all occasions. All plankton samples were carefully examined and extraneous material, if any, was removed with teflon forceps. Dried samples were then ground to powder with mortar and pestle, reweighed and apportioned into aliquots for elemental and radionuclide analyses. Samples along with appropriate blanks and standards were analyzed for P, Ca, Sr, Fe, Al, Zn, Cu and Mn by atomic absorption and spectrophotometric techniques. Thorium-234 was measured by non-destructive beta assay (Krishnaswami et al., 1976), ^{210}Pb and ^{210}Po by total alpha counting techniques (Cherry and Heyraud, 1981), and ^{228}Th, ^{230}Th, ^{232}Th, and ^{238}U by radiochemical purification and alpha spectrometry (Krishnaswami et al., 1976).

Results and discussion

The concentrations of various elements and natural radionuclides in zooplankton species and salps are given in Tables 1 and 2. The concentrations of Ca, Sr, Al, Fe, Mn, Cu and Zn in the zooplankton samples (Table 1) are

Table 1. Elemental and radionuclide concentrations in zooplankton samples

Species	Collection date	μg g⁻¹ dry								dpm g⁻¹ dry					
		P	Ca⁺	Sr⁺	Fe	Al	Zn	Cu	Mn	²³⁴Th	²²⁸Th*	²³²Th*	²³⁸U	²¹⁰Po**	²¹⁰Pb*
Amonalocera patersoni	13.4.84	8699	3531	46	191	240	436	19.3	5.2	18.7	0.035	0.025	0.103	37.7	0.47
	24.4.84	7790	11793	194	306	206	187	8.6	9.5	NM	0.101	0.012	0.279	20.9	0.24
Crab larvae (species unknown)	24.4.84	9159	51681	829	85	227	74	14.0	8.7	5.7	0.133	0.029	0.045	17.5	ND
Mixed copepods (600–2000 μm)	4.5.84	8711	3829	49	248	486	299	10.1	7.4	11.6	0.034	0.018	0.750	28.2	0.95
	8.5.84	7767	6699	80	278	511	355	16.5	8.9	18.7	0.127	0.027	0.137	18.0	0.29

*Errors in these measurements are large (30–50%) because of low signals.
**Errors are approximately ± 4%.
+Values are salt corrected based on measured Na content.
NM = not measured; ND = not detectable.

Table 2. Elemental and radionuclide concentrations in salps

Species	Collection date	μg g⁻¹ dry								dpm g⁻¹ dry					
		P	Ca⁺	Sr⁺	Fe	Al	Zn	Cu	Mn	²³⁴Th	²²⁸Th*	²³²Th*	²³⁸U	²¹⁰Po**	²¹⁰Pb*
Thalia democratica	13.4.84	5892	66581	1905	940	205	93	17.5	36.0	17	0.164	0.042	1.33	20.1	0.38
	16.4.84	8731	63998	1571	2005	1528	312	21.8	84.0	111	0.295	0.159	1.05	NM	NM
	24.4.84	5411	59310	1390	269	619	94	17.0	20.9	23	0.155	0.094	0.88	16.6	0.31
	4.5.84.	10228	63852	1174	4078	3052	163	22.4	79.0	58				18.1	2.53
Salpa maxima	8.5.84	1866	12821	30.7	1154	1034	35.6	7.3	40.9	90.5	0.428	0.186	0.26	9.9	4.37

*Errors in these measurements are large (30–50%) because of very low signals.
**Errors are approximately ± 7%.
+Values are salt corrected based on measured Na content.
NM = not measured.

similar to those reported by Martin and Knauer (1973). Our data show that by and large elemental abundances in the galatinous salps are of the same order as those in crustacean zooplankton. Geometric mean enrichment factors (metal/Al ratio in organisms divided by metal/Al ratio in crustal rock) computed for salps are ^{210}Po=800, Sr=164, Zn=140, Ca=101, ^{210}Pb=55, U=35, Cu=26, Mn=4.3, Th=4.1, Fe=1.9. Whereas Mn, Fe and Th show little if any enrichment in salps relative to crustal rock, the high enrichment factors for Ca, Sr, Zn, Cu, U, ^{210}Po and ^{210}Pb could result from either some degree of biological uptake by physiological processes or from the food they filter from seawater. Analyses of salp body samples without the gut contents would help to resolve this issue. In the case of Cu and Zn, concentrations in salps exhibit a good correlation with P concentration suggesting their involvement in the processes of active biological uptake. In general quite comparable enrichment factors are found for the zooplankton species listed in Table 1 (i.e. ^{210}Po=3100, Zn=880, Sr=88, Cu=63, Ca=57, ^{210}Pb=52, U=22, Th=2.4, Mn=2.2 and Fe=0.96), and they are of the same order as the enrichment factor values for zooplankton reported by Cherry et al. (1983). However, the geometric mean enrichment factor for ^{210}Po in salps (800) is lower than the geometric mean value (3100) computed for our samples of crustacean zooplankton. Typical ^{210}Po enrichment factors of 4000 were reported for zooplankton by Cherry et al. (1983) but their compilation did not include data for gelatinous species like salps. The lower ^{210}Po enrichment factor in salps as well as a lower geometric mean ^{210}Po/^{210}Pb ratio in salps (14) than in the crustacean zooplankton species (60) indicate most likely a richer alumino-silicate component in salps than in the zooplankton listed in Table 1. The higher Al content in salps (Table 2) relative to zooplankton (Table 1) lends support to this contention.

Salps produce an abundance of fecal pellets or flakes which are large and settle very rapidly (Bruland and Silver, 1981; Madin, 1982). In fact, the sinking rate of salp fecal pellets are the fastest recorded among zooplankton species (Angel, 1984). These considerations alone suggest that material transport through salp feces could be significant in controlling the distribution and removal of elements from the water column. Elemental and radionuclide concentrations in salps and their fecal pellets are given in Table 3. It is evident that for most nuclides there is considerable enrichment in the fecal material of salps. For example, except for P and Sr, feces/salp ratios for the elements and radionuclides were > 1 indicating higher nuclide concentrations in fecal pellets than in the organisms which produced them (Table 3). The only other data on radionuclide concentrations are those of Heyraud (1982) who reported ^{210}Po and ^{210}Pb levels of 35 ± 7 and 20 ± 10 dpm/g dry in the feces of *Salpa maxima*, values nearly identical to the concentrations measured in this study (Table 3). One possible explanation for the lower nuclide abudances in salps relative to their feces is the dilution of the gut contents by salp body. Similar observations have been noted for trace

Table 3. Range and mean elemental and radionuclide concentration in salps (n=5), their feces and the estimated flux contribution due to defecation

Nuclide	Salps (μg g^{-1} dry)		Salp feces	Feces/Salps	Flux via defecation
	Range	Geometric mean	(μg g^{-1} dry)		(μg g^{-1} dry salp d^{-1})
P	1866–10228	5560	3621	0.65	905
Ca	12821–63998	46041	82378	1.8	20595
Sr	30.7–1905	684	415	0.6	104
Fe	269–4078	1190	11818	9.9	2955
Al	205–3052	906	28490	31	7123
Zn	35.6–312	110	196	1.8	49
Cu	7.3–22.4	16.0	34.3	2.1	8.6
Mn	20.9–84.0	45.9	169.0	3.7	42.0
^{234}Th	17–111	47*	750*	16	187.0**
^{228}Th	0.155–0.428	0.238*	2.16*	9.1	0.54**
^{232}Th	0.042–0.186	0.104*	1.01*	9.7	0.25**
^{238}U	0.26 –1.33	0.75*	0.97*	1.3	0.24**
^{210}Po	9.9 –20.1	15.6*	39.5*	2.5	9.9**
^{210}Pb	0.31 –4.37	1.1*	24.0*	22	6.0**

* In units of dpm g^{-1} dry wt.
** In units of dpm g^{-1} dry d^{-1}.

elements and radionuclides in fecal pellets of euphausiid crustaceans (Fowler, 1977; Higgo et al., 1977; 1980; Beasley et al., 1978) and copepods (Fowler, 1982; Fowler et al., 1983). Particularly noteworthy with salp feces is the fact that it contained 2.84% Al, 1.2% Fe and 4 μg g^{-1} ^{232}Th, concentrations which indicate a high alumino-silicate content. Based on Al and Th abundances in crustal rocks and salp feces, the alumino-silicate content in feces is calculated to be in the range of 32.8–35.8%. In this regard, Wallace et al. (1981) measuring Al profiles in the Gulf Stream found an exponential decrease in particulate Al between 30 and 100 m. They hypothesized that the first order removal of Al in this region could be due to sinking fecal pellets, particularly those of salps. In California current waters the scavenging and rapid removal of ^{234}Th from the surface layer was interpreted to occur in response to intense grazing and fecal pellet production by salps (Coale and Bruland, 1985). Our finding of high Al concentrations (2.84%) and 234Th activity (750 dpm/g) clearly demonstrates the feasibility of this removal mechanism.

Although quantitative biological data on feeding behaviour of Mediterranean salps are lacking, it is possible to derive estimates of element and radionuclide cycling rates through salps using measured nuclide concentrations in salp feces and published salp fecal pellet production rates from other oceanic areas. Madin (1982) has measured the defecation rate of seven species of salps; these rates range between 3.7–27.7 μg fecal C/mg body C/hr. Assuming a defecation rate of 10 μg fecal C/mg body C/hr for *Thalia democratica* and a carbon abundance of 25% dry weight both in fecal pellets (Bruland and Silver, 1981) and in salps (Madin, 1982; our data for weight loss

on ignition), the defecation rate translates to about 250 mg dry feces/g dry salp/day. The elemental and radionuclide fluxes calculated using this defecation rate are given in Table 3. Calcium concentration in salps and corresponding Ca flux via fecal pellets are quite high. If this is due to ingestion of coccolithophores which are quite common in oligotrophic waters of the Mediterranean, then salps may contribute significantly to the carbonate flux from surface to deep waters. For certain elements such as Cu and Zn, the estimated fluxes through salps are nearly the same as those that were computed for defecation from euphausiids (Fowler, 1977). However, where comparisons can be made for the same elements and radionuclides (e.g. Sr, Fe, Mn, ^{210}Po, ^{210}Pb, ^{232}Th and ^{238}U), fluxes through salps ranged from 3 to 35 times greater than corresponding fluxes through euphausiids from the same waters in the Mediterranean (Fowler, 1977; Beasley et al., 1978; Higgo et al., 1980). Since the nuclide concentrations in fecal pellets from both zooplankters are roughly similar (with the exception of Cu and Zn which are much higher in euphausiid pellets), the large observed differences in flux are due primarily to the 5-fold higher computed defecation rate in salps (25% body dry weight/day) compared to that tof the euphausiid *Meganyctiphanes norvegica* ($\sim$ 5% body dry weight/day, Small et al. 1973).

Despite differences in filtering rates and resultant defecation rates between pelagic salps and crustaceans, the question remains as to the relative importance of salps in terms of total biomass compared with other common pelagic crustaceans like copepods and euphausiids. Copepods have classically been considered as the primary consumers of phytoplankton in oceanic waters; however, it is well-known that salps often occur in swarms reaching densities as high as 275 individuals m^{-3} (see Madin, 1974), and in fact in some areas like the Scotia Sea/Antarctic Peninsula region they dominate the zooplankton community at certain times of the year (Huntley et al., 1984). Furthermore Harbison and Gilmer (1976) have shown that a single individual of a large oceanic salp (*Pegea confederata*) has the equivalent grazing impact of at least 450 large calanoid copepods. They also point out that salps which are sparsely distributed in chains in the ocean are rarely sampled in plankton tows, a fact which strongly suggests that their biomass may be greatly underestimated.

The ability of salps to continuously filter particles ranging in size from 1 μm to 1 mm (Madin, 1974; Harbison and McAlister, 1979) indicates that small, nuclide-enriched particles of both inorganic and organic origin will be packaged in their fecal pellets. Nothing is known about the fate of the pellet-associated nuclides following release from salps, but owing to the high sinking rates of salp pellets (up to 2700 m day^{-1}, Bruland and Silver, 1981), they have the potential to rapidly transport incorporated trace elements and radionuclides to great depth. The observation of intact salp fecal flakes in sediment traps at 900 m (Iseki, 1981) supports this hypothesis. Equally possible is that during descent and subsequent dissolution, a fraction of the nuclides may be released to the water column in a manner similar to that which has been

observed to occur in fecal pellets from other zooplankton species (Heyraud et al., 1976; Fowler, 1982). Clearly, the biogeochemical control that salp feces may exert on the fate and distribution of elements and radionuclides in oceanic waters warrants further study.

Acknowledgements

References

Alldredge, A.L. and L.P. Madin. 1982. Pelagic tunicates: Unique herbivores in the marine plankton. Bioscience 32:655–663.

Angel, M.V. 1984. Detrital organic fluxes through pelagic ecosystems. In: M.J.R. Fasham (ed.), Flows of Energy and Materials in Marine Ecosystems, pp. 475–516. Plenum Press, New York.

Beasley, T.M., M. Heyraud, J.J.W. Higgo, R.D. Cherry and S.W. Fowler. 1978. ^{210}Po and ^{210}Pb in zooplankton fecal pellets. Marine Biology 44:325–328.

Braconnot, J.C. 1971. Contribution à l'étude biologique et écologique des Tuniciers pélagiques Salpides et Doliolides, I. Hydrologie et écologie des Salpides. Vie et Milieu 22 (2, Ser. B): 257–286.

Bruland, K.W. 1983. Trace elements in sea-water. In: J.P. Riley and R. Chester (eds.), Chemical Oceanography, Vol. 8, pp. 157–220, Academic Press, London.

Cherry, R.D., M. Heyraud and J.J.W. Higgo. 1983. Polonium-210: its enrichment in the hepatopancrease of marine invertebrates. Marine Ecology Progress Series 13:229–236.

Coale, K.H. and K.W. Bruland. 1985. ^{234}Th:^{238}U disequilibria within the California current. Limnology and Oceanography 30:22–33.

Collier, R., and J.M. Edmond. 1984. The trace element geochemistry of marine biogenic particulate matter. Progress in Oceanography 13:113–199.

Deuser, W.G., P.G. Brewer, T.D. Jickells and R.F. Commeau. 1983. Biological control of removal of abiogenic particles from the surface ocean. Science 219:388–391.

Deuser, W.G., E.H. Rosss and R.F. Anderson. 1981. Seasonality in the supply of sediment to the deep Sargasso Sea and implication for the rapid transport of matter to the deep ocean. Deep-Sea Research 28:495–505.

Fowler, S.W. 1977. Trace elements in zooplankton particulate products. Nature 269:51–53

Fowler, S.W. 1982. Biological transfer and transport processes. In: G. Kullenberg (ed.), Pollutant Transfer and Transport in the Sea, Vol. II, pp. 1–65, Chemical Rubber Company, Boca Raton, Florida.

Fowler, S.W., S. Ballestra, J. La Rosa and R. Fukai. 1983. Vertical transport of particulate-associated plutonium and americium in the upper water column of the Northeast Pacific. Deep-Sea Research 30:1221–1233.

Fowler, S.W. (in press). Trace metal monitoring of pelagic organisms from the open Mediterranean Sea. Environmental Monitoring and Assessment.

Harbison, G.R. and R.W. Gilmer. 1976. The feeding rates of the pelagic tunicate *Pegea confederata* and two other salps. Limnology and Oceanography 21:517–528.

Harbison, G.R. and V.L. McAlister. 1979. The filter-feeding rates and particle retention efficiencies of three species of Cyclosalpa (Tunicata, Thaliacea). Limnology and Oceanography 24:875–892.

Heyraud, M., 1982. Contribution a l'etude du polonium-210 et du plomb-210 dans les organismes marins et leur environnement. These de Doctorat d'Etat es Sciences Naturelles, Universite Pierre et Marie Curie, Paris 6, 144 p.

Heyraud, M., S.W. Fowler, T.M. Beasley and R.D. Cherry. 1976. [210]Po in euphausiids: A detailed study. Marine Biology 34:127–136.

Higgo, J.J.W., R.D. Cherry, M. Heyraud, S.W. Fowler, 1977. Rapid removal of plutonium from the oceanic surface layer by zooplankton faecal pellets. Nature 266:623–624.

Higgo, J.J.W., R.D. Cherry, M. Heyraud, S.W. Fowler, and T.M. Beasley. 1980. The vertical oceanic transport of alpha radioactive nuclides by zooplankton fecal pellets. In: Natural Radiation Environment III, Vol. 1 T.F. Gesell, and W.M. Lowder (eds.), pp. 502–513. NTIS CONF-780422, Washington, D.C.

Huntley, M., V. Marin, P. Sykes, and R. Rohan. 1984. Antarctic salps. II. Trophodynamics. EOS, Transactions, American Geophysical Union 65:922.

Iseki, K. 1981. Particulate organic matter transport to the deep sea by salp fecal pellets. Marine Ecology Progress Series 5:55–60.

Krishnaswami, S., D. Lal and B.L.K. Somayajulu. 1976. Investigations of gram quantities of Atlantic and Pacific surface particulates. Earth and Planetary Science Letters, 32:403–419.

La Rosa, J. 1976. A simple system for recovering zooplanktonic fecal pellets in quantity. Deep-Sea Research 23:995–997.

Lowman, F.G., T.R. Rice and F.A. Richards. 1971. Accumulation and redistribution of radionuclides by marine organisms. In: Radioactivity in the Marine Environment, Chap. 7, National Academy of Sciences, Washington, D.C.

Madin, L.P. 1974. Field observations on the feeding behaviour of salps (Tunicata: Thaliacea) Marine Biology 25:143–147.

Madin, L.P. 1982. Production, composition and sedimentation of salp fecal pellets in oceanic waters. Marine Biology 67:39–45.

Martin, J.H. and G.A. Knauer. 1973. The elemental composition of plankton. Geochimica et Cosmochimica Acta 37:1639–1653.

Small, L.F., S.W. Fowler, and S. Keckes. 1973. Flux of zinc through a macroplanktonic crustacean. In: Radioactive Contamination of the Marine Environment, pp. 437–452. International Atomic Energy Agency, Vienna.

Wallace, G.T. Jr., O.M. Mahoney, R. Dulmage, F. Storti and N. Dudek. 1981. First-order removal of particulate aluminium in oceanic surface layers. Nature 293:729–731.