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Biological factors affecting variability of persistent pollutant levels in cetaceans[1]

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ABSTRACT

The main biological factors responsible for the variability of pollutant concentrations in cetaceans are reviewed. Diet is significant because many pollutants are concentrated through food webs. This explains most interspecific differences in pollutant levels and it may also contribute to variation among populations of the same species or even among different components of the same population when diet is subject to age-related or sex-related variations. The effect of body size is complex. Excretion rate and activity of detoxifying enzymes decrease as body weight increases, processes which would lead to higher pollutant concentrations in large animals. In contrast, a high metabolic rate, which is inversely correlated to body size, is associated with high pollutant concentrations. These opposing effects usually result in higher residue levels in smaller individuals. Body composition affects the contribution of each body compartment to the overall pollutant load. Therefore, the body load of lipophilic pollutants will strongly depend on the relative mass of blubber, a variable that shows a threefold variation among cetacean species or, in seasonal feeders, among individuals. Nutritive condition also affects the dynamics of lipophilic pollutants. Lipid mobilisation results in an increase in residue levels, but this variation is not as large as a purely concentrative model would suggest because of enhancement of detoxification processes following a rise in tissue pollutant concentrations. Disease affects pollutant levels in different ways: impoverishing nutritive condition; altering normal physiological functions; and depressing reproduction therefore reducing reproductive transfer in females. The combined result of these processes is usually an increase in pollutant levels in diseased individuals. The concentration of lipophilic pollutants normally increases with age in males because input exceeds the ability of the organism to excrete pollutants. Variable proportions of the pollutant load are transferred to offspring during gestation and lactation, for which reason tissue concentrations in females decrease or stabilise, thus producing lower residue levels than in males. However, because not all compounds are transferred at the same rate, their relative abundance varies with age and sex. Intensity of reproductive transfer is also associated with the reproductive traits of the species, particularly the length of lactation. With the exception of zinc, concentrations of heavy metals increase with age in both sexes but, by contrast with lipophilic pollutants, concentrations in females are similar or higher than in males. The significance of these factors of variation should be taken into account when designing sampling methodology, comparing sample groups, or evaluating toxicological impact.

KEYWORDS: POLLUTION; HEAVY METALS; ORGANOCHLORINES; REPRODUCTION; BIOACCUMULATION; BIOMAGNIFICATION; CETACEANS-GENERAL; BOTTLENOSE DOLPHINS; HARBOUR PORPOISE; SPOTTED DOLPHIN; MINKE WHALE; FIN WHALE; SPERM WHALE; RIGHT WHALE; BOWHEAD WHALE

INTRODUCTION

Exposure of a given organism to a given pollutant is commonly monitored through the concentration of the targeted pollutant in selected tissues of the organism. This is clearly easier and more straightforward than measuring direct intake through food or other sources

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of exposure and has been used extensively to monitor population exposure and to identify components of the ecosystem that are susceptible to pollutants.

However, when a sufficiently large number of individuals belonging to the same population have been studied, a substantial variation in tissue residue levels has been observed. This suggests that components of the same population, although sharing the same ecosystem, are not identically exposed to xenobiotics and that their capacity to excrete these pollutants is also different. Proper knowledge of the patterns of variation of pollutant levels within populations is necessary in order to assess the impact of xenobiotics.

During the 1970s, the discovery that some cetacean species carried extremely high levels of pollutants in their tissues, particularly heavy metals and organochlorines, raised concerns about the effects of these compounds on their survival, particularly in association with other threats including direct exploitation, incidental mortality in fishing gear and destruction of habitat. This led to attempts to improve the monitoring of xenobiotic exposure. There is now a considerable body of literature on the tissue levels of isolated individuals or larger samples from cetacean populations. However, results are often difficult to compare and the extent of exposure is difficult to assess because of substantial variation in tissue levels among individuals of different sex, age, reproductive status or nutritive condition. Cetaceans are long-lived and their growth period is protracted. Many are seasonal feeders and their body compositions undergo drastic changes throughout the year, with reproduction involving considerable energy expenditure and transfer of organic constituents to offspring. These factors combine to create large individual variation in pollutant levels.

The present paper reviews information available on sources of individual variation of pollutant levels in cetaceans. This is relevant not only to the design of surveys in this field, but also to the reliable assessment of population exposure to a given compound.

MAIN FACTORS AFFECTING INDIVIDUAL VARIATION

Diet

Most persistent contaminants are incorporated into the body of mammals via food, and thus in pollution studies of cetaceans it has been accepted as a general axiom that diet determines the xenobiotic load of a species. While this may not be always true[2], in absolute terms, intake via food represents the bulk of pollutant intake.

The effect of diet is particularly significant because many persistent pollutants increase their concentrations through the food web, and therefore tissue concentrations in top predators are much higher than those in organisms feeding at low trophic levels. This increase in concentration of a substance in an organism compared to that in its food is commonly known as biomagnification and it depends on a variety of factors. In small animals with gills, equilibrium partitioning of chemicals between body lipids and the environment appears to be the main factor regulating pollutant accumulation. However, in air-breathing predators such as marine mammals, biomagnification is thought to occur because the mass of the pollutant is largely conserved along the food chain, while the food through which it is transferred is partly transformed into energy or excreted (Janssen *et al.*, 1993).

Biomagnification is usually defined as the ratio of concentrations between predator and prey. However, this is rather simplistic because other factors, such as the physical and chemical properties of the compound, the existence of other routes of exposure and/or the physiological and biochemical make-up of the animal also play a significant role in the

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[2] Rawson *et al.* (1995) have suggested that inhalation is a significant source of HgSe in bottlenose dolphins.

process. This explains the increasing criticism that models based on simplistic assumptions of food chain structure have attracted in recent years (Janssen *et al.*, 1993; James and Kleinow, 1994).

The potential for biomagnification varies greatly among pollutants. It is generally accepted that it is high for most organochlorine compounds, particularly those with high molecular weight and abundant chlorine substitutions, e.g. DDT, many PCBs, chlordane, toxaphene (especially nonachlorobornanes) and polychlorinated terphenyls (PCTs). Among the PCBs, biomagnification potential varies with structure and it has been shown that congeners with vicinal unsubstituted positions (especially *meta* and *para*) are selectively metabolised by marine mammals (Boon *et al.*, 1992). Polybrominated biphenyls (PBBs) behave like PCBs. Dibenzodioxins and dibenzofurans are less lipophilic and easier to degrade, so their biomagnification potential appears lower (Ballschmiter *et al.*, 1989; Rappe and Buser, 1989). Heavy metals constitute a heterogeneous group. Mercury is usually accepted as being bioaccumulative, whereas cadmium is not; data on lead and zinc are inconclusive (Laws, 1981; Kay, 1985; Bowles, 1999). Taking into account the limited information available, it appears that the potential for biomagnification of radionuclides and polyaromatic hydrocarbons (PAHs) by marine mammals is low (Anderson *et al.*, 1990; Calmet *et al.*, 1992). In general, fish are considered to be better metabolisers of PAHs than molluscs, for which reason it is likely that biomagnification of these compounds will be lower in fish-eating cetaceans than in those feeding on cephalopods (Law and Whinnett, 1992).

However, direct evidence for biomagnification occurring in cetaceans is limited. Table 1 shows available information on tissue levels of some pollutants and concentrations in their food, together with the biomagnification factor. These data should be viewed with some caution because the comparison of the whole prey is usually made against a single tissue of the cetacean. Moreover, the prey analysed, although selected in every case to account for a representative sample of the cetacean diet, clearly will not contain the identical pollutant loads that a cetacean would encounter in diverse combination of prey species. However, the results from the different surveys and species are reasonably consistent and some general patterns may be found. The biomagnification factor of all organochlorine compounds and mercury appears extremely high (on several occasions exceeding over 100-fold), whereas elements such as chromium, nickel, copper, zinc, cadmium and lead approached unity (and indeed were quite often lower than one), suggesting that biomagnification does not occurr for these elements.

For those pollutants in which biomagnification is significant, diet is undoubtedly a key factor determining resultant tissue concentrations. Indeed, it is expected to explain most of the interspecific variation occurring in cetacean species inhabiting the same waters. However, irrespective of the overall biomagnification factors, some organisms may display a specificity for the accumulation of a given compound and this may lead to increased levels of such a compound in subsequent levels of the food chain. For example, nickel levels in baleen whales are comparatively higher than those in toothed whales because of the ability of krill to concentrate this metal.

It is important, however, to remember that diet may vary substantially at the intraspecific or even intrapopulation levels. In particular, variation in diet associated with age and sex, especially in sexually dimorphic species, has been reported for a number of species, including sperm whales (Clarke *et al.*, 1993), white whales (Seaman *et al.*, 1982), spotted dolphins (Bernard and Hohn, 1989) and harbour porpoises (Recchia and Read, 1989). This variation may be caused by the lower diving capacity of the smaller individuals and the resultant differences in prey size by younger individuals, or differential requirements in composition of diet during different growth or reproductive states. Such shifts in diet may,

Table 1

Biomagnification factors (available in the literature) of cetaceans in relation to their food. Factors are calculated from concentrations expressed on an extractable lipid basis in the case of organochlorines and on a fresh weight basis in the case of trace elements. m: muscle; l: liver; k: kidney; Magn: magnification factor; N: number.

Compound	Species	N	Tissue	N	Food	Magn.	Reference
PCB	*D. leucas*	-	blubber	-	fish	8.0	Muir *et al.* (1992)
	T. truncatus	1	blubber	2	fish	510.6	Morris *et al.* (1989)
	S. coeruleoalba	1	blubber	2	fish	21.6	Morris *et al.* (1989)
		1	blubber	-	squid + fish	11.0	Tanabe *et al.* (1981b)
	P. phocoena	4	blubber	2	fish	38.9	Morris *et al.* (1989)
tDDT	*D. leucas*	-	blubber	-	fish	10.0	Muir *et al.* (1992)
	T. truncatus	1	blubber	2	fish	569.3	Morris *et al.* (1989)
	S. coeruleoalba	1	blubber	2	fish	70.5	Morris *et al.* (1989)
		1	blubber	-	squid + fish	12.0	Tanabe *et al.* (1981b)
	P. phocoena	4	blubber	2	fish	19.8	Morris *et al.* (1989)
HCB	*D. leucas*	-	blubber	-	fish	3.0	Muir *et al.* (1992)
	T. truncatus	1	blubber	2	fish	89.9	Morris *et al.* (1989)
	S. coeruleoalba	1	blubber	2	fish	56.1	Morris *et al.* (1989)
		1	blubber	-	squid + fish	23.0	Tanabe *et al.* (1981b)
	P. phocoena	4	blubber	2	fish	27.4	Morris *et al.* (1989)
tHCH	*D. leucas*	-	blubber	-	fish	1.4	Muir *et al.* (1992)
	S. coeruleoalba	1	blubber	-	squid + fish	6.4	Tanabe *et al.* (1981b)
Dieldrin	*T. truncatus*	1	blubber	2	fish	1,723.9	Morris *et al.* (1989)
	S. coeruleoalba	1	blubber	2	fish	64.3	Morris *et al.* (1989)
	P. phocoena	4	blubber	2	fish	65.2	Morris *et al.* (1989)
Total-Hg	*M. monoceros*	-	liver	-	fish	163.0	Muir *et al.* (1992)
	S. coeruleoalba	6	m+l+k	5	squid	125.0	Itano *et al.* (1984b)
		6	m+l+k	10	fish	175.0	Itano *et al.* (1984b)
		1	muscle	2	fish	8.0	Morris *et al.* (1989)
	T. truncatus	1	muscle	2	fish	10.0	Morris *et al.* (1989)
		1	muscle	-	fish	24.0	Moreno *et al.* (1984)
	P. phocoena	2	muscle	2	fish	9.0	Morris *et al.* (1989)
Methyl-Hg	*S. coeruleoalba*	4	m+l+k	5	squid	57.0	Itano *et al.* (1984a)
		4	m+l+k	10	fish	69.0	Itano *et al.* (1984a)
Cd	*M. monoceros*	-	liver	-	fish	80.0	Muir *et al.* (1992)
	S. coeruleoalba	25	muscle	3	squid	0.0	Honda and Tatsukawa (1981)
		25	liver	3	squid	0.4	Honda and Tatsukawa (1981)
		25	muscle	2	fish	2.5	Honda and Tatsukawa (1981)
		25	liver	2	fish	263.0	Honda and Tatsukawa (1981)
Cu	*S. coeruleoalba*	25	muscle	3	squid	0.1	Honda and Tatsukawa (1981)
		25	liver	3	squid	0.2	Honda and Tatsukawa (1981)
		25	muscle	2	fish	0.9	Honda and Tatsukawa (1981)
		25	liver	2	fish	3.0	Honda and Tatsukawa (1981)
		1	muscle	2	fish	0.6	Morris *et al.* (1989)
	T. truncatus	1	muscle	2	fish	0.7	Morris *et al.* (1989)
	P. phocoena	1	muscle	2	fish	0.6	Morris *et al.* (1989)
Fe	*S. coeruleoalba*	25	muscle	3	squid	2.1	Honda and Tatsukawa (1981)
		25	liver	3	squid	2.9	Honda and Tatsukawa (1981)
		25	muscle	2	fish	15.0	Honda and Tatsukawa (1981)
		25	liver	2	fish	20.1	Honda and Tatsukawa (1981)
Mn	*S. coeruleoalba*	25	muscle	3	squid	0.6	Honda and Tatsukawa (1981)
		25	liver	3	squid	6.7	Honda and Tatsukawa (1981)
		25	muscle	2	fish	0.2	Honda and Tatsukawa (1981)
		25	liver	2	fish	2.1	Honda and Tatsukawa (1981)

continued

Table 1 continued

Compound	Species	N	Tissue	N	Food	Magn.	Reference
Ni	*S. coeruleoalba*	25	muscle	3	squid	0.6	Honda and Tatsukawa (1981)
		25	liver	3	squid	1.5	Honda and Tatsukawa (1981)
		25	muscle	2	fish	0.8	Honda and Tatsukawa (1981)
		25	liver	2	fish	2.0	Honda and Tatsukawa (1981)
		1	muscle	2	fish	1.0	Morris *et al.* (1989)
	T. truncatus	1	muscle	2	fish	1.0	Morris *et al.* (1989)
	P. phocoena	2	muscle	2	fish	0.7	Morris *et al.* (1989)
Pb	*M. monoceros*	-	liver	-	fish	0.1	Muir *et al.* (1992)
	S. coeruleoalba	25	muscle	3	squid	0.7	Honda and Tatsukawa (1981)
		25	liver	3	squid	2.0	Honda and Tatsukawa (1981)
		25	muscle	2	fish	0.4	Honda and Tatsukawa (1981)
		25	liver	2	fish	1.3	Honda and Tatsukawa (1981)
		1	muscle	2	fish	0.9	Morris *et al.* (1989)
	T. truncatus	1	muscle	2	fish	0.9	Morris *et al.* (1989)
	P. phocoena	2	muscle	2	fish	0.7	Morris *et al.* (1989)
Zn	*S. coeruleoalba*	25	muscle	3	squid	0.3	Honda and Tatsukawa (1981)
		25	liver	3	squid	1.2	Honda and Tatsukawa (1981)
		25	muscle	2	fish	1.2	Honda and Tatsukawa (1981)
		25	liver	2	fish	4.0	Honda and Tatsukawa (1981)
		1	muscle	2	fish	0.4	Morris *et al.* (1989)
	T. truncatus	1	muscle	2	fish	0.4	Morris *et al.* (1989)
	P. phocoena	2	muscle	2	fish	0.8	Morris *et al.* (1989)
Se	*S. coeruleoalba*	6	m+l+k	5	squid	9.0	Itano *et al.* (1984a)
		6	m+l+k	10	fish	7.0	Itano *et al.* (1984a)

on some occasions, involve substantial variation in the type of organism consumed or even in the trophic level exploited. For example, after being weaned, juvenile harbour porpoises base their diet on euphausiids while their mothers are feeding on euphausiid predators (Smith and Read, 1992). In addition, lactating spotted dolphins consume mainly fish, whereas pregnant females feed almost exclusively on squid in order to cope with different nutritional requirements at each reproductive stage (Bernard and Hohn, 1989). This may have consequences not only for the absolute amount of pollutants ingested, but also on their relative abundance. For example, cadmium tissue concentrations in species consuming squid are higher because this prey carries high levels of this metal (Szefer *et al.*, 1994).

These age- or sex-related variations in diet undoubtedly influence intrapopulation variation in pollutant levels, although the recognition of this effect may be complex unless shifts in diet are longstanding. For example, Tanabe *et al.* (1984) found that younger Southern Hemisphere minke whales carried higher concentrations of DDTs and PCBs in their tissues than mature ones. This contrasts with what would be expected according to typical age-related trends in males of other species, and this author associated this apparent anomaly with a shift in diet with age. Thus, immature minke whales remain at lower latitudes during the summer and feed not only on euphausiids but also on copepods and fish, whereas adult individuals migrate to higher latitudes and base their diet solely on (less polluted) euphausiids.

Finally, it should be taken into account that diet is also likely to affect the activity of enzymes responsible for detoxification. For example, the MFO system is a multi-enzymatic substrate-inducible complex and has been found to be more active in species with a wide dietary spectrum than in those that feed on a limited number of species. MFO induction is also dependent on the type of food consumed. The ability to detoxify foreign compounds is higher in herbivores than in carnivores because the former are more often exposed to natural toxic chemicals than the latter. This link between an ability for detoxification and diet has been put forward to explain differences in adaptation to pollution in a number of avian and mammalian species (e.g. Walker, 1980; Focardi *et al.*, 1988; Fossi *et al.*, 1988) and is also likely to play a role in the dynamics of pollutants in cetaceans.

Body size

Body size plays a complex role in interspecific variation in the accumulation pattern of pollutants. On the one hand, the elimination rate of foreign compounds per unit body weight in mammals decreases as body weight increases (Parke, 1980). This is also true for the activity of detoxifying enzymes, particularly microsomal mono-oxygenase systems which contain cytochrome P450 forms (Walker, 1980). These two factors would, in principle, combine to favour the accumulation of higher pollutant levels in species of large size. On the other hand, however, there is an inverse relationship between metabolic rate and body size and, because metabolic rate is also usually correlated with an ability to accumulate pollutants in vertebrates (Moriarty, 1984), higher pollutant accumulation rates are in principle to be expected in smaller species.

Although these two effects are opposed, in most species the influence of the metabolic rate outstrips that of the other two factors combined. Thus, in models of pollutant accumulation, the concentration factor is largely dependent on the predator's daily rate of food consumption as a proportion of the predator's body weight (inversely correlated to body size) and, of course, on the mean concentration of pollutant within the prey (Moriarty, 1984). Therefore, smaller animals overall tend to carry larger body loads of pollutants relative to their body weight in spite of high enzymatic activity and elimination rates.

Variation in body size among cetaceans is dramatic. Some representatives of the families Delphinidae, Phocoenidae and Pontoporidae weigh, when adult, only about 30-40kg, while the larger Balaenopterids can reach a body mass exceeding 150 metric tonnes (Evans, 1987). This represents about a 4×10^3 increase, by far the largest variation range in any mammal taxon. This of course has consequences for observed interspecific variation in pollutant levels. For example, Henry and Best (1983) found in southern Africa that minke whales (*ca* 10 tonnes) carried about 50% higher DDT concentrations in their blubber than fin whales (*ca* 80 tonnes), despite both being krill-eating species. Moreover, dieldrin was detected in measurable quantities in minke whales but not in fin whales. In the North Atlantic, Borrell (1993b) found that blubber organochlorine concentrations in male sperm whales (*ca* 50 tonnes) were about 20% of those found in male long-finned pilot whales (*ca* 1.5 tonnes) from the same waters, again despite the fact that both species are teutophagous and therefore feed on similar food resources.

The effect of body mass is not usually taken into account when studying interspecific variation in pollutant levels, and much of the observed variation is usually attributed to dissimilarities in diet. This lack of information makes it difficult to predict the actual influence of body mass on pollutant residue concentrations. A simple model can be proposed if it is accepted that the body load of a given pollutant is directly proportional to the amount of that pollutant absorbed by the intestine. In turn, assuming a given concentration of pollutant in the food, the quantity of pollutant absorbed is directly proportional to the amount of food ingested. Efficiency of food assimilation in cetaceans has been suggested to be about 80% (Lockyer, 1981), but a similar figure is not available for most pollutants. Although the amount of biomass of food ingested will of course depend on a number of factors such as the availability and quality (mainly calorific content) of that food, it is directly proportional to the metabolic rate of the individual and therefore its body mass. Thus, the biomass of food ingested (I) relative to body mass (M) has been calculated (Innes *et al.*, 1986) as:

$$I = 0.42M^{0.67}$$

where I is expressed in kg per day and M in kg.

The mean tissue concentration of a given persistent pollutant in the body of a mammal can be calculated as:

Mean tissue concentration = pollutant body load ÷ body weight

Taking this into account, the relationship between tissue concentration of a given pollutant, the body load of this pollutant and the body mass of the species concerned, can be assumed to vary following the pattern in Fig. 1. This shows that once body size reaches over 10,000kg, mass is of little importance in determining tissue concentrations. In smaller species, however, the effect of body size on the relationship is dramatic. As a consequence of a rapid increase in metabolic rates at lower body mass, both body loads and, particularly, tissue concentrations, increase remarkably. Indeed, this effect is probably more significant in explaining variations in tissue concentrations of different species found in the same waters than small differences in diet or in other biological traits.

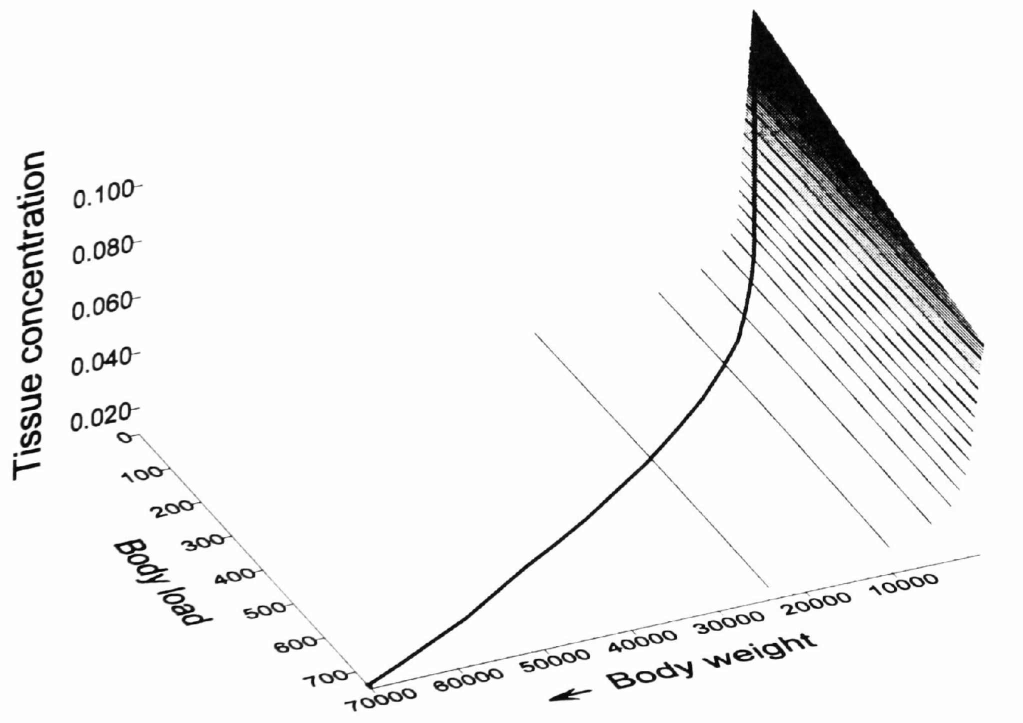

Fig. 1. Theoretical relationship between body mass, body load of a given pollutant, and tissue concentration of that pollutant in the body of a cetacean.

Body composition

The distribution pattern of pollutants in the body of an organism is complex, but largely depends upon the physical and chemical properties of the compounds involved. Some pollutants, such as organochlorines, organobromines and polyaromatic hydrocarbons, are lipophilic and therefore accumulate in fat-rich tissues. This property means that an organism with a large fat compartment will have a large capacity for retaining these chemicals (Aguilar, 1985). Thus, about 70-95% of the total body load of lipophilic xenobiotics in cetaceans is located in the blubber (Table 2). Non-lipophilic pollutants depend on more complex rules of accumulation, although their distribution patterns still follow chemical affinities. Mercury, cadmium, zinc and other heavy metals accumulate mainly in the liver, muscle and kidneys (i. e. Honda *et al.*, 1982; André *et al.*, 1990a). However, others behave differently. For example, lead is mostly retained in bone because its biochemical behaviour is similar to that of calcium, and in man 90% of the lead present in the body is contained in bone. Furthermore, the biological half-life of lead in bone is about five years, while that in soft tissues is only 3-4 weeks (Fridberg, 1985). Radionuclides accumulate more readily in liver than in muscle (Calmet *et al.*, 1992).

Table 2

Contribution of main body compartments to the total load of pollutants present in the bodies of cetaceans. n.a.: not analysed.

Number	Compound	% Blubber	% Muscle	% Liver	% Kidney	% Bone	% Intestine	% Lung	Reference
S. coeruleoalba									
1	tDDT	95.10	4.30	0.20	0.20	n.a.	n.a.	n.a.	Tanabe *et al.* (1981a)
	PCB	95.00	4.60	0.10	0.10	n.a.	n.a.	n.a.	Tanabe *et al.* (1981a)
	BHC	90.00	8.40	0.40	0.30	n.a.	n.a.	n.a.	Tanabe *et al.* (1981a)
	tHCH	91.30	6.50	0.80	0.40	n.a.	n.a.	n.a.	Tanabe *et al.* (1981a)
S. coeruleoalba									
1	tDDT	93.50	4.60	0.23	0.73	n.a.	n.a.	n.a.	Fukushima and Kawai (1981)
	PCB	92.10	6.20	0.53	0.61	n.a.	n.a.	n.a.	Fukushima and Kawai (1981)
	BHC	92.00	5.60	0.67	0.45	n.a.	n.a.	n.a.	Fukushima and Kawai (1981)
S. coeruleoalba									
25	tDDT	96.94	1.81	1.21	0.05	n.a.	n.a.	n.a.	Borrell (1993b)
	PCB	95.58	2.91	1.54	0.09	n.a.	n.a.	n.a.	Borrell (1993b)
M. stejnegeri									
1	tDDT	98.40	1.40	0.08	0.01	n.a.	n.a.	n.a.	Miyazaki *et al.* (1987)
	PCB	97.80	2.00	0.20	0.02	n.a.	n.a.	n.a.	Miyazaki *et al.* (1987)
G. melas									
20	tDDT	99.50	0.40	0.09	0.04	n.a.	n.a.	n.a.	Borrell (1993b)
	PCB	99.00	0.85	0.12	0.03	n.a.	n.a.	n.a.	Borrell (1993b)
B. physalus									
26	tDDT	78.30	12.30	0.10	0.10	9.20	n.a.	n.a.	Aguilar and Borrell (1994a)
	PCB	76.50	13.90	0.10	0.10	9.40	n.a.	n.a.	Aguilar and Borrell (1994a)
S. coeruleoalba									
14	Hg	4.49	57.79	27.93	n.a.	n.a.	n.a.	n.a.	Itano *et al.* (1984a)
14	Se	14.91	37.28	25.35	n.a.	n.a.	n.a.	n.a.	Itano *et al.* (1984a)
11	Methyl-Hg	2.20	88.40	3.37	n.a.	n.a.	n.a.	n.a.	Itano *et al.* (1984a)
S. attenuata									
44	Hg	38.05	26.52	29.72	n.a.	n.a.	1.27	2.04	André *et al.* (1990a)
S. attenuata									
27	Cd	n.a.	18.62	23.63	2.63	n.a.	18.25	9.22	André *et al.* (1990b)

This heterogeneous affinity of pollutants for different parts of the body and the relative importance of these different parts in relation to body mass are significant factors determining the amount of pollutants retained by an organism. In cetaceans, the relative contribution of most tissues and organs to the composition of the body is relatively constant, the only significant difference being blubber. In general, large species tend to have less blubber relative to body mass (Ryg *et al.*, 1993). For example, the percentage of blubber mass in relation to body mass in northern Atlantic waters may increase from 15-19% in large baleen whales (Lockyer, 1976; Lockyer and Waters, 1986) to 25% in medium-sized odontocetes such as pilot whales (Lockyer, 1993) and 45% in harbour porpoises (Slijper, 1958), the smallest of the odontocetes inhabiting the region.

Substantial variation may also be found both among different taxonomic groups and among individuals or species subject to different climates. In right and bowhead whales, both members of the family Balaenidae, blubber constitutes about 40-45% of body mass (Lockyer, 1976; George *et al.*, 1988), while in fin or sei whales of similar mass belonging to the Balaenopteridae, it only contributes about 15-19% (Lockyer, 1976; Lockyer and Waters, 1986). In beaked whales inhabiting cold waters (e.g. northern bottlenose whales), the contribution of blubber to body mass is 40-45% (Benjaminsen and Christensen, 1979), but it is as low as 20-22% in temperate water beaked whales such as Cuvier's or Blainville's (Ross, 1984).

The implications of such variation for the accumulation rates of lipophilic xenobiotics in cetaceans have not been investigated thus far, but it is likely that the fatter the individual, the higher its pollutant load, as has been observed in fish, birds and terrestrial mammals (Samiullah, 1990).

In addition, body composition affects the relative contribution of each body part to the overall pollutant body load. Table 2 details the available information on the percentage contribution of five main body parts to pollutant load in cetaceans. As mentioned above, blubber contributes to the bulk of organochlorine contaminant load, both because of its lipid richness and its large contribution to body mass. Although the lipid content of muscle is low, it is also an important reservoir of organochlorines because of its large contribution to body mass. In some cetaceans (mainly the baleen whales and large toothed whales) bone is very porous and contains abundant lipid reserves; in these cases, bone also contains a significant portion of the total organochlorine load. The contribution from liver, kidneys and other viscera is negligible. Although the data are limited, it appears clear that the contribution of blubber load of organochlorines to total body load is much higher in the small or medium-sized odontocetes (90-99%) than in the larger fin whale (76-78%), as expected from the blubber mass/body mass relationships mentioned above. Data on trace elements are unfortunately not available to allow comparison among species, although muscle appears to be the compartment containing the largest heavy metal loads.

Nutritive condition

As seen above, fat is one of the main constituents of the cetacean body. One of its major functions is to serve as an energy store, for which reason its contribution to body mass strongly depends on the condition of the individual. In species subject to strict seasonal migratory and feeding regimes (e.g. most baleen whales), body fat may vary dramatically through the year. It has been calculated that some baleen whales increase their body weight by 50-100% by the end of the feeding period, mainly because of fat accumulation (Lockyer and Brown, 1981). Indeed, the massive size of baleen whales has been associated with the need to accumulate substantial amounts of lipid reserves to cope with migratory and reproductive requirements during periods of low or no feeding (Brodie, 1975).

Variation in nutritive condition affects not only the volume of the fat compartment but also its composition. Thus, in baleen whales, blubber lipid richness may vary from over 88% in a fat, pregnant female, to as low as 34% in a resting, post lactating whale (Aguilar and Borrell, 1990). Similar, although less marked, variations may be observed in the lipid content of other tissues. Muscle of the posterior part of the trunk in pregnant whales accumulates

17-19% of lipid, whereas in lactating females it only averages 11.5% (Lockyer, 1987). Changes in the lipid content of bone, kidneys and other organs are also significant and have been described in a number of species.

Seasonal fluctuations in the nutritive condition of odontocetes do not appear to be as large as in mysticetes. Variation in blubber thickness is usually moderate and not strictly related to reproductive status, indicating that adequate food supply is generally available to provide the energetic requirements. Changes in lipid content and mass of internal organs are also moderate when compared to baleen whales (Gambell, 1972; Read, 1990; Lockyer, 1993).

It is obvious that variation in lipid richness has implications for the dynamics of lipophilic contaminants, although the actual effects on tissue concentrations induced by this variation are not so clear. When lipids are mobilised, two extreme processes are possible: either pollutants leave the tissues together with the lipids to which they are bound, or they remain in the tissue. In the first case, tissue concentrations will remain constant; in the second, they will increase proportionally to the amount of lipids mobilised. Studies suggest that, despite substantial variability between species or even within individuals, the actual process lies somewhere between the two extremes. In other words, lipid mobilisation results in an increase in the levels of residues, but the variation is not as high as a purely concentrative model would suggest. The reasons for this intermediate accumulative process are unclear, but it appears that partial mobilisation of the more polar fraction of the xenobiotic load and enhancement of metabolising and excretory capabilities when tissue pollutant concentrations rise, attenuates the increase produced by lipid mobilisation (Aguilar, 1987).

Calculation of tissue xenobiotic concentrations in relation to the lipid content of the tissue instead of its fresh weight partially account for such variations, but do not totally solve the problem. The relationship between PCB concentrations in the blubber (expressed on a lipid basis) and the lipid content of this tissue, in a sample of Mediterranean striped dolphins (Aguilar and Borrell, 1994a) shows that even taking into consideration blubber lipid richness, PCB concentrations are negatively correlated with fat content (Fig. 2). This indicates that some build-up of pollutants occurred in dolphins in poor nutritive condition. This increase is due to the fact that lipids are more readily mobilised from the blubber than lipophilic pollutants are and, therefore, the reduction in lipid mass is not coupled with a parallel reduction in xenobiotic mass (Aguilar, 1987). This effect has long been recognised in the dynamics of lipophilic contaminants in marine mammals (e.g. Addison and Smith, 1974; Drescher *et al.*, 1977), and has critically complicated surveys in which substantial variation of nutritive condition of individuals occurred (e.g. Hall *et al.*, 1992; Kuiken *et al.*, 1994).

It is unclear whether changes in nutritive condition may affect tissue concentrations of non-lipophilic pollutants. The most extensive mass changes when a cetacean grows thin or fat occur in the blubber, and therefore these changes mostly affect lipophilic pollutants. However, reduction of protein mass and liver enlargement in individuals in poor nutritive condition are also recognised in mammals (Spinage, 1985; Ortiz, 1987; Watkins *et al.*, 1991). Such changes are likely to influence the dynamics of accumulation of certain non-lipophilic pollutants that concentrate in these tissues, such as most heavy metals (see Table 2). Further research should be carried out to ascertain the effect of mass change in tissues other than blubber on the compartmentation and mobilisation of non-lipophilic pollutants.

Incidence of disease

Most pollutant surveys in cetaceans undertaken to date have been carried out on stranded specimens. Although in most cases the cause of death of these animals is unknown, except in areas where fishing interactions are frequent, disease is certainly the most likely source of mortality (except perhaps, in cases of mass strandings). There are several reasons why a

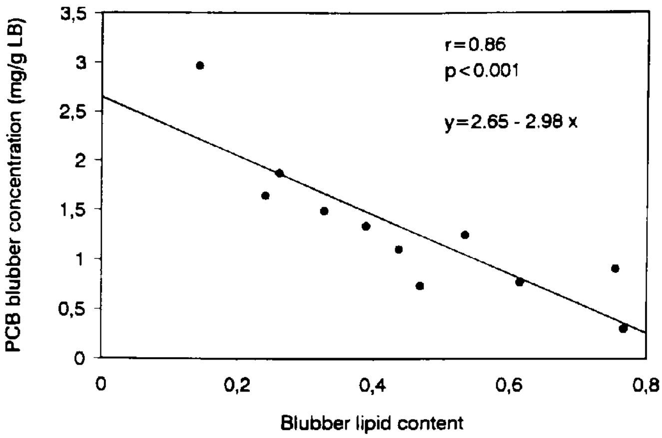

Fig. 2. Relationship between PCB concentration in the blubber of 15-19 year old male Mediterranean striped dolphins, expressed on a lipid basis, and the lipid content of the tissue.

diseased cetacean may be likely to carry abnormal pollutant loads in its body. For example, an animal that has been sick for a long period is likely to be undernourished or to have fed on food resources different from those that constitute its usual diet. In addition, many diseases affect metabolic centres and thus the capacity to metabolise or excrete pollutants may be affected. Therefore, it is questionable whether the pollutant concentrations in the tissues of these cetaceans are representative of normal conditions. The effects of a shift in diet or of fat mobilisation on tissue xenobiotic levels, particularly of those that are lipophilic, have been discussed above. In general terms it is to be expected that a rise in concentrations occur when the individual grows thin. However, the effects of physiological or metabolic alterations remain mostly unclear.

In females subject to severe long-term disease, it is likely that reproduction is altered or discontinued. In these situations, age-related accumulation trends will shift from the usual decreasing pattern in females to one of progressive accumulation, similar to that typical of males. For example, Martineau *et al.* (1987) found that DDT and PCB concentrations increased with age in stranded female white whales from the St Lawrence Estuary. An effect of this type probably explains the abnormally high levels of organochlorines observed in stranded female cetaceans, which in some cases even exceeded those of males (e.g. common dolphins in O'Shea *et al.*, 1980).

The results of studies performed on marine mammals affected by viral epizootics in recent years have repeatedly indicated increased concentrations of pollutants in individuals killed by the disease than in those that survived it (Kuehl *et al.*, 1991; 1994; Hall *et al.*, 1992; Aguilar and Borrell, 1994a). The existence of a cause-effect relationship between susceptibility to the disease and abnormally high pollutant levels has been the subject of substantial controversy and remains unclarified (Kennedy, 1999). Possible explanations include depressed immunocompetence caused by pollutants, mobilisation of pollutants stored in reserve tissues in individuals thinned by the disease, or alterations in physiological functions leading to increased concentrations (Aguilar and Borrell, 1994a).

Lipophilic xenobiotics, both because of the immunodepressive capacity of some of them and their association with lipid dynamics (and therefore with nutritive condition) have centred most discussions on the effect of disease on pollutant levels or vice versa. It is likely, however, that many other pollutants may be affected when the normal physiological functions are altered. Further research is needed to clarify this subject, particularly if stranded cetaceans are to be used for monitoring population exposure.

Age and sex

Most cetaceans inhabit locations far from point sources of pollution and are therefore only affected by xenobiotics that are persistent, i.e. those that are not readily decomposed by the environment (once released). In many cases, particularly for highly lipophilic chemicals, persistence is associated with being accumulative, which means that the pollutant is retained by body tissues and its half-life in the organism is long.

By definition, for a pollutant to be accumulative, its input should in principle exceed the ability of the organism to excrete it. In other words, its intake rate should be initially greater than the combination of its metabolisation and excretion rates. In this situation, concentrations in tissues are expected to increase progressively with age throughout the life of the individual, the slope of the increase being proportional to the difference between the intake rate and the excretion plus metabolisation rates. This increase is further enhanced by the limited ability of foetuses and calves to biotransform xenobiotics. In humans, for example, cytochrome P450 activities are 20-50% of adult activities during the foetal stage (Sipes and Gandolfi, 1991). No similar calculations have been performed for cetaceans, but the activity of degradative enzymes in foetal minke whales (*Balaenoptera acutorostrata*) has been found to be extremely low (Goksøyr *et al.*, 1988). This handicapped detoxification ability is related to the biochemical differentiation of both the rough and smooth endoplasmic reticulum of hepatocytes, which is not complete during the early stages of life.

However, almost invariably, homeostatic responses elicit physiological mechanisms to counteract or destroy unwanted chemicals. When these mechanisms are successful, the initial increase in tissue concentrations levels off and the organism reaches an equilibrium in which enhanced degradation capabilities balance new pollutant intake. In this situation, the slope of the relationship between age and tissue pollutant concentrations tends to level off in older individuals.

Therefore, the pattern of variation of a given pollutant depends on its difficulty of excretion, its capacity to activate metabolisation processes and its resistance to these processes. While the physical and chemical properties of the different xenobiotics are very variable, the physiology of the detoxification processes is quite homogeneous among taxonomically related species. For this reason, age-related patterns observed for a given compound are similar among different cetacean species. Furthermore, transfer during gestation and lactation to offspring plays a key role in determining age-related trends in the tissue concentration of certain pollutants in females. Moreover, a marked difference between males and females in the toxicologic response to a number of xenobiotics has been noted. Capacity for detoxification in female mammals is usually lower than in males. Apparently, the balance between male and female sex hormones is important in determining the activity of cytochrome P450 and other enzymes responsible for pollutant degradation (Sipes and Gandolfi, 1991). Therefore, both sexes should be examined separately.

Fig. 3 shows a hypothetical age-relationship of tissue concentrations for organochlorine and other persistent lipophilic pollutants. This has been extracted from commonly observed patterns in different cetacean species available in the literature (Table 3). In males, concentrations tend to increase rapidly during the juvenile stage, but the slope slowly levels off in older individuals until a plateau is reached. This levelling-off is probably a combination of reduced daily feeding rate in adults and enhanced metabolisation and excretion rates when pollutant levels build-up. Table 3 details case-studies available in the literature in which age-related patterns were investigated (only surveys where $n > 20$).

Table 3

Age-related variation in pollutant levels observed in different cetacean species.
*: sample including males and females, n.s.: non significant trend.

Compound	Species	Tissue	Area	No.	Trend	Reference
MALES						
PCB	*B. physalus*	blubber	E.North Atlantic	69	increase	Aguilar and Borrell (1988)
	B. acutorostrata	blubber	Antarctic	20	increase	Tanabe *et al.* (1986)
	B. acutorostrata	blubber	Antarctic	59	increase	Tanabe *et al.* (1995)
	D. leucas	blubber	West Greenland	71	n.s.	Stern *et al.* (1994)
	G. melas	blubber	Faroe Islands.	30	n.s.	Borrell *et al.* (1995a)
	T. truncatus	blubber	E.South Africa	52	increase	Cockcroft *et al.* (1989)
	S. coeruleoalba	blubber	N.W. Mediterranean	38	increase	Borrell (1993b)
	P. phocoena	blubber	Bay of Fundy	61	increase	Gaskin *et al.* (1983)
	P. phocoena	blubber	Scandinavia	34	increase	Kleivane *et al.* (1995)
	P. dalli	blubber	N.W.North Pacific	40	increase	Subramanian *et al.* (1987)
	P. blainvillei	blubber	Northern Argentina	43	n.s.	Borrell *et al.* (1995)
tDDT	*B. physalus*	blubber	E.North Atlantic	69	increase	Aguilar and Borrell (1988)
	B. acutorostrata	blubber	Antarctic	20	increase	Tanabe *et al.* (1986)
	B. acutorostrata	blubber	Antarctic	59	increase	Tanabe *et al.* (1995)
	D. leucas	blubber	West Greenland	71	n.s.	Stern *et al.* (1994)
	G. melas	blubber	Faroe Islands.	30	n.s.	Borrell *et al.* (1995)
	T. truncatus	blubber	E.South Africa	52	increase	Cockcroft *et al.* (1989)
	S. coeruleoalba	blubber	N.W. Mediterranean	38	increase	Borrell (1993b)
	P. phocoena	blubber	Bay of Fundy	60	increase	Gaskin *et al.* (1982)
	P. phocoena	blubber	Scandinavia	34	increase	Kleivane *et al.* (1995)
	P. dalli	blubber	N.W.North Pacific	40	increase	Subramanian *et al.* (1987)
	P. blainvillei	blubber	Northern Argentina	43	increase	Borrell *et al.* (1995)
tHg	*B. acutorostrata*	liver	Antarctic	96	increase	Honda *et al.* (1987)
	P. macrocephalus	muscle	South Australia	313	decrease	Cannella and Kitchener (1992)
	M. monoceros	blubber	Baffin Island	49 *	increase	Wagemann *et al.* (1983)
		muscle	"	58 *	increase	"
		liver	"	38 *	increase	"
		kidney	"	55 *	increase	"
	M. monoceros	muscle	West Greenland	28	increase	Hansen *et al.* (1990)
		liver	"	26	increase	"
		kidney	"	28	increase	"
	P. phocoena	liver	Norway	56	increase	Teigen *et al.* (1993)
		kidney	"	56	n.s.	"
		muscle	Bay of Fundy	22	increase	Gaskin *et al.* (1972)
		muscle	Bay of Fundy	68	increase	Gaskin *et al.* (1979)
		liver	"	44	increase	"
		kidney	"	26	increase	"
Cd	*B. physalus*	liver	E.North Atlantic	35	increase	Sanpera *et al.* (1995)
		kidney	"	36	n.s.	"
	B. acutorostrata	liver	Antarctic	96	inc-dec	Honda *et al.* (1987)
	M. monoceros	blubber	Baffin Island	45 *	decrease	Wagemann *et al.* (1983)
		muscle	"	58 *	increase	"
		liver	"	38 *	decrease	"
		kidney	"	55 *	increase	"
	M. monoceros	muscle	West Greenland	25	n.s.	Hansen *et al.* (1990)
		liver	"	27	increase	"
		kidney	"	28	n.s.	"

continued

Table 3 continued

Compound	Species	Tissue	Area	No.	Trend	Reference
Co	*B. acutorostrata*	liver	Antarctic	96	n.s.	Honda *et al.* (1987)
Cu	*B. physalus*	muscle	E.North Atlantic	29	n.s.	Sanpera *et al.* (1995)
		liver	"	35	n.s.	"
		kidney	"	35	decrease	"
	B. acutorostrata	liver	Antarctic	96	n.s.	Honda *et al.* (1987)
	M. monoceros	blubber	Baffin Island	45 *	n.s.	Wagemann *et al.* (1983)
		muscle	"	58 *	n.s.	"
		liver	"	38 *	n.s.	"
		kidney	"	55 *	n.s.	"
Ni	*B. acutorostrata*	liver	Antarctic	96	n.s.	Honda *et al.* (1987)
Pb	*B. acutorostrata*	liver	Antarctic	96	n.s.	Honda *et al.* (1987)
	M. monoceros	blubber	Baffin Island	45 *	n.s.	Wagemann *et al.* (1983)
		muscle	"	58 *	n.s.	"
		liver	"	38 *	decrease	"
		kidney	"	55 *	n.s.	"
Zn	*B. physalus*	muscle	E.North Atlantic	33	n.s.	Sanpera *et al.* (1995)
		liver	"	35	n.s.	"
		kidney	"	32	increase	"
	B. acutorostrata	liver	Antarctic	96	n.s.	Honda *et al.* (1987)
	M. monoceros	blubber	Baffin Island	45 *	decrease	Wagemann *et al.* (1983)
		muscle	"	58 *	n.s.	"
		liver	"	38 *	n.s.	"
		kidney	"	55 *	n.s.	"
	M. monoceros	kidney	West Greenland	27	n.s	Hansen *et al.* (1990)
Se	*M. monoceros*	blubber	Baffin Island	47 *	n.s.	Wagemann *et al.*(1983)
		muscle	"	58 *	n.s.	"
		liver	"	38 *	decrease	"
		kidney	"	55 *	n.s.	"
	M. monoceros	kidney	West Greenland	27	increase	Hansen *et al.* (1990)
	P. phocoena	liver	Norway	56	increase	Teigen *et al.* (1993)
		kidney	"	56	n.s.	"
FEMALES						
PCB	*B. physalus*	blubber	E.North Atlantic	97	decrease	Aguilar and Borrell (1988)
	D. leucas	blubber	West Greenland	67	decrease	Stern *et al.* (1994)
	G. melas	blubber	Faroe Islands	69	decrease	Borrell *et al.* (1995)
	G. macrorhynchus	blubber	Japan	24	n.s.	Tanabe *et al.* (1987)
	T. truncatus	blubber	E.South Africa	52	decrease	Cockcroft *et al.* (1989)
	S. coeruleoalba	blubber	N.W. Mediterranean	33	decrease	Borrell (1993b)
	S. coeruleoalba	blubber	Japan	40	n.s.	Fukushima and Kawai (1981)
	P. phocoena	blubber	Bay of Fundy	39	n.s.	Gaskin *et al.* (1983)
	P. dalli	blubber	N.W.North Pacific	26	n.s.	Subramanian *et al.* (1987)
	P. blainvillei	blubber	North Argentina	31	n.s.	Borrell *et al.* (1995)
tDDT	*B. physalus*	blubber	E.North Atlantic	97	decrease	Aguilar and Borrell (1988)
	D. leucas	blubber	West Greenland	67	decrease	Stern *et al.* (1994)
	G. melas	blubber	Faroe Islands	69	decrease	Borrell *et al.* (1995)
	G. macrorhynchus	blubber	Japan	24	n.s.	Tanabe *et al.* (1987)
	T. truncatus	blubber	E.South Africa	52	decrease	Cockcroft *et al.* (1989)
	S. coeruleoalba	blubber	N.W. Mediterranean	33	decrease	Borrell (1993b)
	P. phocoena	blubber	Bay of Fundy	55	decrease	Gaskin *et al.* (1982)
	P. dalli	blubber	N.W.North Pacific	26	n.s.	Subramanian *et al.* (1987)

continued

Table 3 continued

Compound	Species	Tissue	Area	No.	Trend	Reference
tHg	*B. acutorostrata*	liver	Antarctic	39	inc-dec	Honda *et al.* (1987)
	P. macrocephalus	muscle	South Australia	100	n.s.	Cannella and Kitchener (1992)
	M. monoceros	blubber	Baffin Island	49 *	increase	Wagemann *et al.* (1983)
		muscle	"	58 *	increase	"
		liver	"	38 *	decrease	"
		kidney	"	55 *	increase	"
	M. monoceros	muscle	West Greenland	31	increase	Hansen *et al.* (1990)
		liver	"	30	increase	"
		kidney	"	32	increase	"
	D. leucas		Canadian Arctic			Wagemann *et al.* (1990)
	P. phocoena	liver	Norway	36	increase	Teigen *et al.* (1993)
		kidney	"	36	n.s.	"
		muscle	Bay of Fundy	45	increase	Gaskin *et al.* (1979)
		liver	"	24	increase	"
Cd	*B. physalus*	liver	E.North Atlantic	35	increase	Sanpera *et al.* (1995)
		kidney	"	35	increase	"
	B. acutorostrata	liver	Antarctic	39	increase	Honda *et al.* (1987)
	M. monoceros	blubber	Baffin Island	45 *	decrease	Wagemann *et al.* (1983)
		muscle	"	58 *	increase	"
		liver	"	38 *	increase	"
		kidney	"	55 *	increase	"
	M. monoceros	muscle	West Greenland	27	n.s.	Hansen *et al.* (1990)
		liver	"	31	n.s.	"
		kidney	"	32	increase	"
Co	*B. acutorostrata*	liver	Antarctic	39	n.s.	Honda *et al.* (1987)
Cu	*B. physalus*	muscle	E.North Atlantic	37	n.s.	Sanpera *et al.* (1995)
		liver	"	37	decrease	"
		kidney	"	36	decrease	"
	B. acutorostrata	liver	Antarctic	39	n.s.	Honda *et al.* (1987)
	M. monoceros	blubber	Baffin Island	45 *	n.s.	Wagemann *et al.* (1983)
		muscle	"	58 *	n.s.	"
		liver	"	38 *	decrease	"
		kidney	"	55 *	n.s.	"
Fe	*B. acutorostrata*	liver	Antarctic	39	increase	Honda *et al.* (1987)
Ni	*B. acutorostrata*	liver	Antarctic	39	n.s.	Honda *et al.* (1987)
Pb	*B. acutorostrata*	liver	Antarctic	39	n.s.	Honda *et al.* (1987)
	M. monoceros	blubber	Baffin Island	45 *	n.s.	Wagemann *et al.* (1983)
		muscle	"	58 *	n.s.	"
		liver	"	38 *	increase	"
		kidney	"	55 *	n.s.	"
Zn	*B. physalus*	muscle	E.North Atlantic	38	decrease	Sanpera *et al.* (1995)
		liver	"	37	n.s.	"
		kidney	"	35	increase	"
	B. acutorostrata	liver	Antarctic	39	n.s.	Honda *et al.* (1987)
	M. monoceros	blubber	Baffin Island	45 *	decrease	Wagemann *et al.* (1983)
		muscle	"	58 *	n.s.	"
		liver	"	38 *	n.s.	"
		kidney	"	55 *	increase	"
	M. monoceros	kidney	"	31	increase	Hansen *et al.* (1990)

continued

Table 3 continued

Compound	Species	Tissue	Area	No.	Trend	Reference
Se	*M. monoceros*	blubber	Baffin Island	47 *	n.s.	Wagemann *et al.* (1983)
		muscle	"	58 *	n.s.	"
		liver	"	38 *	increase	"
		kidney	"	55 *	decrease	"
	M. monoceros	kidney	West Greenland	28	increase	Hansen *et al.* (1990)
	P. phocoena	liver	Norway	36	increase	Teigen *et al.* (1993)
		kidney	"	36	n.s.	"
MALES AND FEMALES TOGETHER						
tHg	*D. leucas*	muscle	West Greenland	24	n.s.	Hansen *et al.* (1990)
		liver	"	23	increase	
		kidney	"	20	increase	"
	D. leucas	muscle	Canadian Arctic and	107	n.s.	Wagemann *et al.* (1990)
		liver	St Lawrence estuary	139	increase	"
		kidney	"	137	increase	"
	G. melas	liver	Faroe Islands	92	increase	Caurant *et al.* (1994)
		kidney	Faroe Islands	54	increase	"
	S. coeruleoalba	blubber	Japan	36	increase	Itano and Kawai (1981)
		muscle	"	38	increase	"
		liver	"	34	increase	"
	S. coeruleoalba	muscle	Japan	51	increase	Honda *et al.* (1983)
		liver	"	45	increase	
		kidney	"	20	increase	"
	S. coeruleoalba	liver	W. Mediterranean	27	increase	André *et al.* (1991)
	S. attenuata	muscle	E. tropical Pacific	31	increase	André *et al.* (1990a)
		liver	"	33	increase	"
		kidney	"	31	n.s.	"
	P. phocoena	muscle	W. Greenland	78	increase	Paludan-Muller *et al.* (1993)
		liver	"	78	increase	"
		kidney	"	78	increase	"
		skin	"	78	increase	"
Methyl-Hg	*S. coeruleoalba*	muscle	Japan	31	n.s.	Itano and Kawai (1981)
As	*G. melas*	liver	Faroe Islands	92	n.s.	Caurant *et al.* (1994)
		kidney	Faroe Islands	97	n.s.	"
Cd	*B. physalus*	liver	Iceland	39	n.s.	Sanpera *et al.* (1995)
		kidney	"	49	n.s.	"
	B. acutorostrata	liver	Antarctic	135	increase	Honda *et al.* (1987)
	D. leucas	muscle	West Greenland	24	n.s.	Hansen *et al.* (1990)
		liver	"	23	increase	"
	D. leucas	muscle	Canadian Arctic and	108	n.s.	Wagemann *et al.* (1990)
		liver	St Lawrence estuary	139	increase	"
		kidney	"	137	increase	"
	G. melas	liver	Faroe Islands	120	increase	Caurant *et al.* (1994)
		kidney	Faroe Islands	97	increase	"
	S. coeruleoalba	muscle	Japan	59	increase	Honda *et al.* (1983)
		liver	"	57	increase	"
		kidney	"	30	n.s.	"
	S. attenuata	muscle	E. tropical Pacific	21	increase	André *et al.* (1990b)
	P. phocoena	muscle	W. Greenland	78	increase	Paludan-Muller *et al.* (1993)
		liver	"	78	increase	"
		kidney	"	78	increase	"
		skin	"	78	increase	"

continued

Table 3 continued

Compound	Species	Tissue	Area	No.	Trend	Reference
Co	*B. acutorostrata*	liver	Antarctic	135	n.s.	Honda *et al.* (1987)
Cu	*B. physalus*	muscle	Iceland	36	decrease	Sanpera *et al.* (1995)
		liver	"	38	n.s.	"
		kidney	"	37	decrease	"
	B. acutorostrata	liver	Antarctic	135	n.s.	Honda *et al.* (1987)
	D. leucas	muscle	Canadian Arctic and	107	decrease	Wagemann *et al.* (1990)
		liver	St Lawrence estuary	139	decrease	"
		kidney	"	137	decrease	"
	G. melas	liver	Faroe Islands	122	increase	Caurant *et al.* (1994)
		kidney	"	97	increase	"
	S. coeruleoalba	muscle	Japan	59	n.s.	Honda *et al.* (1983)
		liver	"	57	decrease	"
		kidney	"	30	decrease	"
Fe	*B. acutorostrata*	liver	Antarctic	135	increase	Honda *et al.* (1987)
	S. coeruleoalba	muscle	Japan	59	increase	Honda *et al.* (1983)
		liver	"	57	n.s.	"
		kidney	"	30	n.s.	"
Ni	*B. acutorostrata*	liver	Antarctic	135	n.s.	Honda *et al.* (1987)
	S. coeruleoalba	muscle	Japan	59	increase	Honda *et al.* (1983)
		liver	"	57	increase	"
		kidney	"	30	n.s.	"
Pb	*B. acutorostrata*	liver	Antarctic	135	n.s.	Honda *et al.* (1987)
	S. coeruleoalba	muscle	Japan	59	increase	Honda *et al.* (1983)
		liver	"	57	increase	"
		kidney	"	30	n.s.	"
Zn	*B. physalus*	muscle	Iceland	33	n.s.	Sanpera *et al.* (1995)
		liver	"	38	decrease	"
		kidney	"	33	n.s.	"
	B. acutorostrata	liver	Antarctic	135	n.s.	Honda *et al.* (1987)
	D. leucas	muscle	West Greenland	24	n.s.	Hansen *et al.* (1990)
		liver	"	23	n.s.	"
		kidney	"	20	n.s.	"
	D .leucas	muscle	Canadian Arctic and	108	n.s.	Wagemann *et al.* (1990)
		liver	St Lawrence estuary	139	n.s.	"
		kidney	"	137	n.s.	"
	G. melas	liver	Faroe Islands	122	n.s.	Caurant *et al.* (1994)
		kidney	"	97	increase	"
	S. coeruleoalba	muscle	Japan	59	decrease	Honda *et al.* (1983)
		liver	"	57	decrease	"
		kidney	"	30	n.s.	"
Se	*D. leucas*	muscle	West Greenland	24	n.s.	Hansen *et al.* (1990)
		liver	"	23	increase	"
		kidney	"	20	n.s.	"
	D. leucas	muscle	Canadian Arctic and	105	n.s.	Wagemann *et al.* (1990)
		liver	St Lawrence estuary	111	n.s.	"
		kidney	"	115	n.s.	"
	G. melas	liver	Faroe Islands	94	increase	Caurant *et al.* (1994)
		kidney	"	54	increase	"
	S. coeruleoalba	blubber	Japan	36	n.s.	Itano and Kawai (1981)
		muscle	"	38	increase	"
		liver	"	34	increase	"

In the great majority of cases a positive correlation was found between age and pollutant concentrations and, when this was not the case, trends were unclear but never indicated a decrease in concentrations.

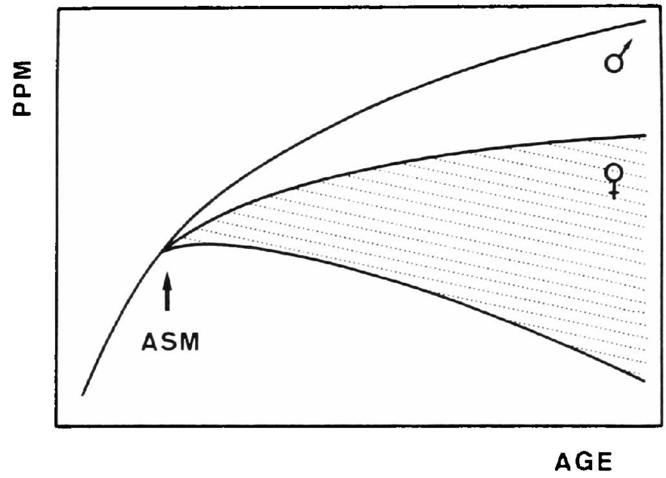

Fig. 3. Typical age-related variation of concentration of organochlorine and other persistent lipophilic pollutants in the tissues of cetaceans.

In females, observed patterns were quite different. Lipophilic chemicals easily traverse placental membranes and are therefore transferred to the foetus. This passage is easier for chemicals of low molecular weight, which in organochlorines is associated with low chlorination of the molecule, than for those with high weight, usually associated with a high number of chlorine substitutions (Juchau, 1983). Moreover, lipophilic compounds are also readily transferred to milk (Ridgway and Reddy, 1995). Again, there are some differences depending on the physical and chemical properties of the compound; the highly chlorinated organochlorines are transferred less efficiently from the body lipid deposits to the circulatory system, and from there to milk, than those lowly chlorinated (Aguilar and Borrell, 1994c).

The discharge occurring during reproduction produces a change in the age-related pattern in females since the onset of reproduction. The initial increase during the juvenile stage slows down and concentrations either increase at a lower rate than in males, stabilise, or decrease (Fig. 3). Logically, the magnitude of this change depends on the intensity of the reproductive transfer and this will, in turn, depend on the physical and chemical properties of the compound and the biological traits of the species involved.

Table 4 details available information on the percentage of organochlorine body load of the female transferred to the offspring during a single pregnancy or lactation. As can be seen, transfer is much larger during lactation (range: 7-98% depending on species and compound) than during pregnancy (range: 0.5-9.4%). This is explained by the large amount of lipids transferred during lactation to the calf, which is much larger than that deposited in the foetus. The total amount of organochlorines transferred during a complete reproductive cycle is estimated to range from 7-100%, depending on species and compound.

However, irrespective of the intensity of this transfer, this discharge will produce lower concentrations of lipophilic pollutants in the tissues of adult females than in those of adult males. Table 5 details differences observed between males and females (only surveys with $n > 25$ were considered). In the totality of the cases, males presented higher concentrations

Table 4

Reproductive transfer of pollutants, calculated as percent transfer in relation to maternal body load, for different pollutants and cetacean species. n: number of individuals used to calculate the pollutant transfer; M: males; F: females; F(l): lactating females; F(p) pregnant females.

	n						Transfer			
Species	F	M	F(l)	milk	F(p)	foetus	Gest.	Lact.	Total	Reference
tDDT										
B. physalus	82	59	-	-	-	-	-	-	11.8	Aguilar and Borrell (1994b)
G. melas	-	-	21	21	11	11	7.8	80.0	87.8	Borrell *et al.* (1995)
T. truncatus	-	-	-	-	-	-	-	-	80.0	Cockcroft *et al.* (1989)
S. coeruleoalba	-	6	7	-	1	1	4.2	91.0	95.2	Fukushima and Kawai (1981)
S. coeruleoalba	1	-	-	1	1	1	4.7	94.6	99.3	Tanabe *et al.* (1981a,1982)
PCB										
B. physalus	82	59	-	-	-	-	-	-	5.3	Aguilar and Borrell (1994)
G. melas	-	-	21	21	11	11	6.1	95.5	101.6	Borrell *et al.* (1995a)
T. truncatus	-	-	-	-	-	-	-	-	80.0	Cockcroft *et al.* (1989)
S. coeruleoalba	-	6	7	-	1	1	3.8	88.0	91.8	Fukushima and Kawai (1981)
S. coeruleoalba	1	-	-	1	1	1	4.0	91.1	95.1	Tanabe *et al.* (1981a,1982)
HCB										
S. coeruleoalba	-	6	7	-	1	1	6.3	72.0	78.3	Fukushima and Kawai (1981)
S. coeruleoalba	1	-	-	1	1	1	9.4	98.0	107.4	Tanabe *et al.* (1981a,1982)
tHCH										
S. coeruleoalba	1	-	-	1	1	1	8.9	93.5	102.4	Tanabe *et al.* (1981,1982)
tOCs										
P. phocoena	-	-	-	-	-	1	15.0	-	-	Duinker and Hillebrand (1979)
Hg										
S. coeruleoalba	-	-	-	-	1	1	0.4	-	-	Itano *et al.* (1984b)
Se										
S. coeruleoalba	-	-	-	-	1	1	0.9	-	-	Itano *et al.* (1984b)
Methyl-Hg										
S. coeruleoalba	-	-	-	-	1	1	1.0	-	-	Itano *et al.* (1984b)

than females. The difference between sexes ranged from about a two-fold variation (Baird's beaked whales from Japan - Subramanian *et al.*, 1988; minke whales from the Antarctic - Tanabe *et al.*, 1986), to over a six-fold variation (bottlenose dolphins from South Africa - Cockcroft *et al.*, 1989; white whales from the St Lawrence - Martineau *et al.*, 1987).

The above mechanisms of accumulation, degradation or excretion obviously affect the various organochlorine compounds in a different manner depending on their chemical structure and physico-chemical properties. As a consequence, their relative abundance in tissues will not only depend on that in the environment, but also on the age, sex and reproductive history of the individual involved. Thus, in marine mammals the ratios tDDT/PCB and DDE/tDDT have usually been found to increase in males and to decrease in females. This obviously results in both ratios being typically higher in adult males than in adult females (Subramanian *et al.*, 1987; Aguilar and Borrell, 1988; Borrell, 1993a; Stern *et al.*, 1994; Borrell *et al.*, 1995; 1996).

In trace elements, age-related variation patterns are not so homogeneous and predictable (Fig. 4). Cadmium and mercury concentrations are low at birth and increase progressively with age in both sexes. Levels of selenium are highly correlated with those of mercury (Koeman *et al.*, 1973) and, therefore, also increase with age. However, for all three elements, the slope of the trend is frequently steeper in females, for which reason adult females often carry higher tissue levels of these three compounds than males (Table 5).

Table 5

Male-female difference in pollutant concentrations determined for various pollutants and cetacean species. n.s.: non significant trend.

Compound/Species	Tissue	Area	No.	Difference	Reference
PCB					
B. physalus	blubber	E.North Atlantic	101	higher in males	Aguilar and Borrell (1988)
B. borealis	blubber	Iceland	40	higher in males	Borrell (1993a)
	blubber	Canadian Arctic	75	higher in males	Muir *et al.* (1990)
	blubber	West Greenland	89	higher in males	Stern *et al.* (1994)
G. melas	blubber	Faroe Islands	99	higher in males	Borrell *et al.* (1995)
T. truncatus	blubber	E.South Africa	31	higher in males	Cockcroft *et al.* (1989)
	blubber	Gulf of Mexico	26	higher in males	Kuehl and Habler (1995)
S. coeruleoalba	blubber	N.W. Mediterranean	58	higher in males	Borrell (1993b)
P. phocoena	blubber	Bay of Fundy	40	higher in males	Gaskin *et al.* (1983)
	blubber	British waters	28	higher in males	Kuiken *et al.* (1994)
	blubber	Denmark	37	higher in males	Clausen and Andersen (1988)
P. dalli	blubber	N.W.North Pacific	27	higher in males	Subramanian *et al.* (1987)
tDDT					
B. physalus	blubber	E.North Atlantic	101	higher in males	Aguilar and Borrell (1988)
B. borealis	blubber	Iceland	40	higher in males	Borrell (1993a)
D. leucas	blubber	Canadian Arctic	75	higher in males	Muir *et al.* (1990)
	blubber	West Greenland	89	higher in males	Stern *et al.* (1994)
G. melas	blubber	Faroe Islands	99	higher in males	Borrell *et al.* (1995)
T. truncatus	blubber	E.South Africa	29	higher in males	Cockcroft *et al.* (1989)
	blubber	Gulf of Mexico	26	higher in males	Kuehl and Habler (1995)
S. coeruleoalba	blubber	N.W. Mediterranean	58	higher in males	Borrell (1993b)
P. phocoena	blubber	Bay of Fundy	47	higher in males	Gaskin *et al.* (1982)
	blubber	Denmark	37	higher in males	Clausen and Andersen (1988)
P. dalli	blubber	N.W.North Pacific	27	higher in males	Subramanian *et al.* (1987)
Dieldrin					
D. leucas	blubber	Canadian Arctic	75	higher in males	Muir *et al.* (1990)
T. truncatus	blubber	Gulf of Mexico	26	higher in males	Kuehl and Habler (1995)
HCB					
D. leucas	blubber	Canadian Arctic	75	higher in males	Muir *et al.* (1990)
P. phocoena	blubber	British waters	28	higher in males	Kuiken *et al.* (1994)
T. truncatus	blubber	Gulf of Mexico	26	n.s.	Kuehl and Habler (1995)
alfa HCH					
D. leucas	blubber	Canadian Arctic	75	n.s.	Muir *et al.* (1990)
P. phocoena	blubber	British waters	28	higher in males	Kuiken *et al.* (1994)
Methyl-Hg					
B. physalus	muscle	N-E Spain	30	n.s.	Sanpera *et al.* (1993)
tHg					
B. physalus	muscle	N-E Spain	30	n.s.	Sanpera *et al.* (1993)
	liver	"	30	n.s.	"
P. macrocephalus	muscle	South Australia	414	higher in females	Cannella and Kitchener (1992)
M. monoceros	muscle	West Greenland	59	higher in females	Hansen *et al.* (1990)
	liver	"	56	higher in females	"
	kidney	"	60	higher in females	"
G. melas	liver	Faroe Islands	92	higher in females	Caurant *et al.* (1994)
	kidney	"	54	n.s.	"
T. truncatus	liver	Gulf of Mexico	27	higher in males	Kuehl and Habler (1995)
S. coeruleoalba	muscle	Japan	51	n.s.	Honda *et al.* (1983)
	liver	"	45	n.s.	"
S. attenuata	muscle	E. tropical Pacific	31	higher in females	André *et al.* (1990a)
	liver	"	33	higher in females	"
	kidney	"	31	higher in females	"

continued

Table 5 continued

Compound/Species	Tissue	Area	No.	Difference	Reference
tHG cont.					
P. phocoena	liver	Norway	92	n.s.	Teigen *et al.*(1993)
	kidney	"	92	n.s.	"
	muscle	Bay of Fundy	113	higher in females	Gaskin *et al.* (1979)
	liver	"	68	higher in males	"
	kidney	"	42	higher in females	"
As					
G. melas	liver	Faroe Islands	92	n.s.	Caurant *et al.* (1994)
	kidney	"	54	n.s.	"
Cd					
B. physalus	liver	E.North Atlantic	70	n.s.	Sanpera *et al.* (1995)
	kidney	"	71	n.s.	"
B. physalus	liver	Iceland	39	n.s.	Sanpera *et al.* (1995)
	kidney	"	49	n.s.	"
G. melas	liver	Faroe Islands	120	higher in females	Caurant *et al.* (1994)
	kidney	"	54	n.s.	"
S. coeruleoalba	muscle	Japan	59	n.s.	Honda *et al.* (1983)
	liver	"	57	n.s.	"
	kidney	"	30	n.s.	"
S. attenuata	muscle	E. tropical Pacific	27	n.s.	André *et al.* (1990b)
	liver	"	27	n.s.	"
	kidney	"	27	n.s.	"
Cu					
B. physalus	muscle	E.North Atlantic	66	higher in males	Sanpera *et al.* (1995)
	liver	"	72	n.s.	"
	kidney	"	71	n.s.	"
B. physalus	muscle	Iceland	36	n.s.	Sanpera *et al.* (1995)
	liver	"	38	higher in males	"
	kidney	"	37	n.s.	"
G. melas	liver	Faroe Islands	120	higher in females	Caurant *et al.* (1994)
	kidney	"	97	n.s	"
S. coeruleoalba	muscle	Japan	59	n.s.	Honda *et al.* (1983)
	liver	"	57	higher in males	"
	kidney	"	30	n.s.	"
Fe					
B. acutorostrata	liver	Antarctic ocean	135	higher in males	Honda *et al.* (1987)
S. coeruleoalba	muscle	Japan	59	n.s.	Honda *et al.* (1983)
	liver	"	57	higher in males	"
	kidney	"	30	n.s.	"
Mn					
S. coeruleoalba	muscle	Japan	59	n.s.	Honda *et al.* (1983)
	liver	"	57	higher in females	"
	kidney	"	30	n.s.	"
Ni					
S. coeruleoalba	muscle	Japan	59	higher in males	Honda *et al.* (1983)
	liver	"	57	higher in males	"
	kidney	"	30	n.s.	"
Pb					
S. coeruleoalba	muscle	Japan	59	higher in males	Honda *et al.* (1983)
	liver	"	57	higher in males	"
	kidney	"	30	n.s.	"

continued

Table 5 continued

Compound/Species	Tissue	Area	No.	Difference	Reference
Zn					
B. physalus	muscle	E.North Atlantic	71	n.s.	Sanpera *et al.* (1995)
	liver	"	69	n.s.	"
	kidney	"	67	n.s.	"
	muscle	Iceland	35	n.s.	Sanpera *et al.* (1995)
	liver	"	35	n.s.	"
	kidney	"	33	n.s.	"
G. melas	liver	Faroe Islands	120	n.s.	Caurant *et al.* (1994)
	kidney		97	n.s.	"
S. coeruleoalba	muscle	Japan	59	n.s.	Honda *et al.* (1983)
	liver	"	57	higher in males	"
	kidney	"	30	n.s.	"
Se					
G. melas	liver	Faroe Islands	92	higher in females	Caurant *et al.* (1994)
	kidney	"	54	n.s.	"
P. phocoena	liver	Norway	92	n.s.	Teigen *et al.* (1993)
	kidney	"	92	n.s.	"

This difference exists despite the fact that there is apparently no impediment to the transplacental transport of these elements and that transfer to milk occurs, although it is reduced. The only information on percentage of body load transfer through reproduction available for cetaceans is the study by Itano *et al.* (1984b) on striped dolphins, which indicated a gestational transfer of only 0.4-1% of maternal load of mercury and selenium to the foetus. The ratio foetal concentration/maternal concentration for a given tissue is also indicative of gestational transfer. Honda and Tatsukawa (1981) and Honda *et al.* (1986) calculated these ratios for a number of heavy metals in the striped dolphin and found values usually below unity, which indicates that some restriction exists for the placental passage of these elements.

Data on lactational transfer are even more sparse. No calculations on percentage of body load of trace elements through milk are available for cetaceans. In humans, maternal milk usually contains about 5% of the mercury concentration of maternal blood (Goyer, 1991). In cetaceans, information on heavy metal content in milk is restricted to a single study on mercury and selenium in the striped dolphin (Itano *et al.*, 1984b) but extremely low levels of lactational transfer are suggested.

It appears that it can be generally accepted that the reproductive transfer of mercury, selenium or cadmium is negligible and unlikely to affect the elemental load of the mother. Although this would explain a similarity in levels of these chemicals in both sexes, it does not justify the higher tissue concentrations usually detected in females. The cause for this dissimilarity remains unclear. It has been suggested that in sexually dimorphic species, it is due to the dilution of elements in the body of the males, which are larger (Caurant *et al.*, 1994). However, this does not explain maintenance of the difference in the long-term, neither does it explain the fact that the same difference has been observed in species which are not sexually dimorphic (Table 5), such as the spotted dolphin and harbour porpoise. Indeed, it is more likely that this age-related variation is associated with a difference in metabolic pathways linked to hormone cycles, obviously different in both sexes, as suggested by Caurant *et al.* (1994).

A significant portion of the mercury present in the tissues of marine mammals is found speciated, mainly as methylmercury (CH_3Hg), a much more toxic form than inorganic mercury. Information about sex or age-related trends in concentrations of speciated forms is

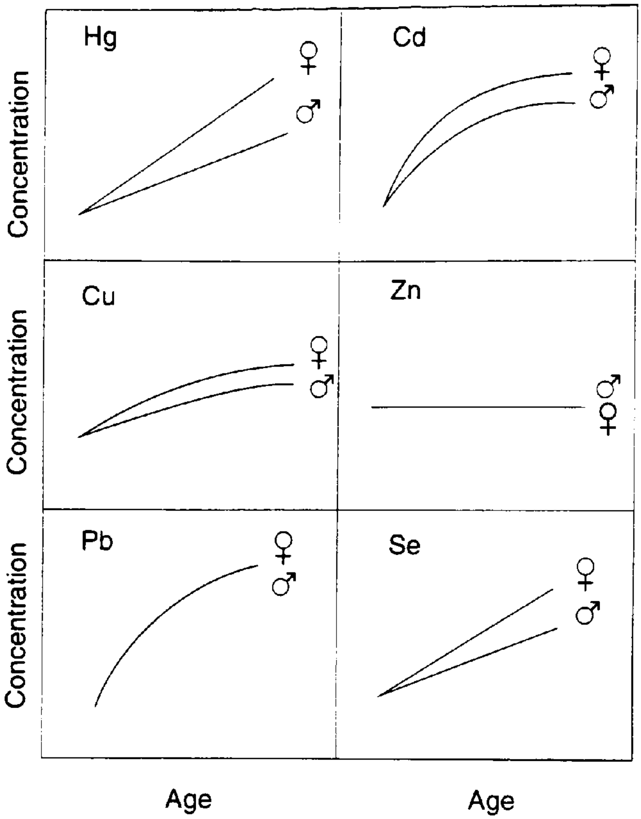

Fig. 4. Typical age-related variation of concentration of selected trace elements in the tissues of cetaceans.

scarce and limited to CH_3Hg, which also appears to increase with age in both sexes (Reijnders, 1980; Sanpera *et al.*, 1993). However, marine mammals have a well known ability to demethylate CH_3Hg and, because this process is progressive throughout the life of the individual, its relative abundance, as measured by the index $\%CH_3Hg/tHg$, has been found to decrease with age (Reijnders, 1980).

Lead behaves differently however. In mammals its concentration in different tissues follows variable age-related trends, but it accumulates markedly in bone and kidneys (Goyer, 1991). Therefore, body loads tend to progressively accumulate throughout life, although a levelling-off of this increasing trend may occur at advanced ages (Fig. 4). Lead is able to cross the placenta and it may be found in the milk in low quantities (Honda *et al.*, 1983; 1987; André *et al.*, 1990a). Usually, levels in males are somewhat higher than in females (Tables 3 and 5) although the information available is insufficient to allow reliable quantification of reproductive transfer.

Data on other heavy metals is more sparse. Copper often shows modest increases with age although in some cases it may be stable throughout the life of the individual or even decrease (Table 3 and Fig. 4). It readily passes the placental membranes and levels in the foetus are usually higher than in the mother (Fujise *et al.*, 1988; Law *et al.*, 1992). However, in terms of body loads, this transfer is probably negligible and tissue concentrations are generally slightly higher in males than in females (Table 5). This difference is apparently due to sex-related differences in hormone metabolism (Caurant *et al.*, 1994) as suggested for mercury and cadmium. Zinc did not show any trend associated with age and no differences were found between the sexes. Placental transfer is apparently low (Law *et al.*, 1992). Data on cobalt, arsenic and nickel are insufficient to draw conclusions about age-related or sex-related variations in cetaceans, although data from other mammals suggest that, if existing, these should be moderate (Goyer, 1991).

No information is available on age- or sex-related variation in either sex or reproductive transfer of radionuclides, polyaromatic hydrocarbons or hydrocarbons in general.

Reproductive biology

As seen above, some pollutants are transferred from the reproducing female to the offspring, both during gestation and lactation. There is considerable uniformity in the basic traits associated with pregnancy in cetaceans. Thus, the duration of gestation and the size of neonates relative to that of their mothers, and therefore the relative amount of biomass transferred, are generally constant (Perrin and Reilly, 1984). In contrast, there is large variability among species in the duration of lactation and, consequently, in the amount of biomass transferred. In baleen whales, lactation is short and typically extends over a period of about 5-10 months (Lockyer, 1984), apparently because transition to independent feeding does not require complex learning. In toothed whales, in contrast, behaviour associated with capture of prey is complex, requires considerable training and lactation is therefore more protracted (Brodie, 1969). Its duration ranges from slightly over one year in small delphinidae to about 7-13 years in sperm whales (Best *et al.*, 1984; Perrin and Reilly, 1984).

This large variation in the length of lactation entails substantial interspecific variation in the amount of pollutants transferred. Indeed, in those chemicals that are excreted with the milk, like most lipophilic compounds, reproductive transfer is directly related to duration of lactation. Fig. 5 shows the relationship between the extent of the adult male-female difference in the levels of PCBs and lactation length in nine cetacean species. Pollutant data for producing this relationship have been extracted from Table 5, and lactation length of the various species from Braham (1984), Gaskin *et al.* (1984), Lockyer (1984) and Perrin and Reilly (1984). There is a significant ($p < 0.05$) correlation between the two variables, the sex-related difference being low in baleen whales and other cetaceans with short lactation periods, but high in small delphinidae with protracted lactation lengths.

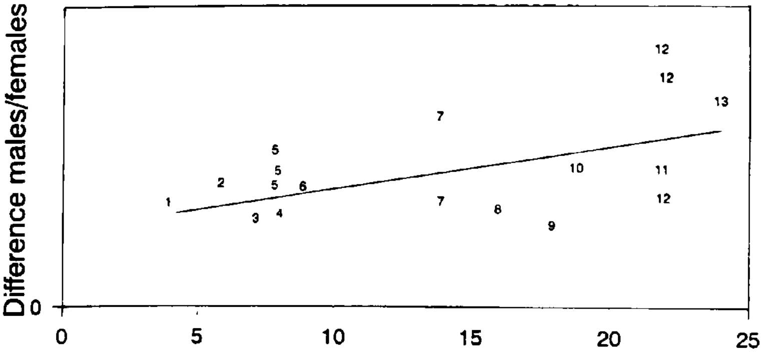

Fig. 5. Relationship between length of lactation and adult male-female differences in PCB blubber concentrations in different species of cetaceans. $y = 1.76 + 0.081x$; $r = 0.53$; $p < 0.05$.

Key: 1 = *B. acutorostrata*; 2 = *B. borealis*; 3 = *E. robustus*; 4 = *B. physalus*; 5 = *P. phocoena*; 6 = *P. blainvillei*; 7 = *S. coeruleoalba*; 8 = *D. delphis*; 9 = *L. acutus*; 10 = *G. macrorhynchus*; 11 = *G. melas*; 12 = *D. leucas*; 13 = *P. dalli*.

In addition, the relative proportion of the organochlorine load transferred to offspring was estimated to be much lower in fin whales (range 3-27%) than in bottlenose dolphins (*ca* 80%) or striped dolphins (72-91%), again reflecting differences in the length of lactation period (Aguilar and Borrell, 1994c). Furthermore, the age-related patterns of variation of pollutant levels in females may reflect changes in reproductive activity with age. For example, Tanabe *et al.* (1987) found that, after the typical decrease in organochlorine concentrations that follow the beginning of reproduction in adult female short-finned pilot whales, a secondary increase appeared in individuals above the age of 25, which corresponds to a slowing-down of reproductive activity in the species.

IMPLICATIONS OF THE EXISTENCE OF INDIVIDUAL VARIABILITY

Sampling techniques and source

As mentioned above, many surveys attempt to monitor pollutant levels in cetacean populations using stranded individuals. This approach has a number of drawbacks, some of which can be readily solved if factors inducing individual variation are taken into account, while others are more difficult or impossible to overcome. The significance of disease and nutritive condition on the tissue levels has already been discussed and their effect may (or may not) be accounted for if corrections for lipid content of the tissues or proper identification of cause of death is possible. However, strandings also suffer from a number of other shortcomings, as discussed below.

The age composition of stranded cetaceans reflects the pattern of the age-specific mortality rate rather than the actual age-structure of the population. Neonates, weaners and senescent individuals are usually more common among strandings than juveniles and young mature animals, which comprise most of the actual population. In some conditions, even the sex ratio may be biased. Calzada *et al.* (1994) examined the age and sex composition of the striped dolphins killed by the 1990-1992 Mediterranean morbillivirus epizootic and found an abnormally high relative abundance of calves and old individuals in the sample. Similar results were obtained by Härkönen and Heide-Jørgensen (1990) in a similar study on the 1988 harbour seal epizootic in the Kattegat-Skagerrak area.

Another problem is that samples from stranded cetaceans are almost invariably collected at unknown post-mortem times and this is likely to have an effect on tissue pollutant concentrations. Some organic compounds are very volatile and they may abandon the cellular structure if the carcass is subject to direct sun or wind exposure, conditions likely to occur in a stranded cetacean. Borrell and Aguilar (1990) examined variation in organochlorine levels in tissues from a dolphin corpse left outdoors and found that the lipid content and concentrations of DDTs and PCBs significantly decreased in muscle and blubber after a few days of exposure to temperate weather conditions. Although similar studies have not been carried out on other organic pollutants or on heavy metals, it is likely that changes of this nature may also occur for these compounds.

The combined effect of these factors is difficult to predict. Impoverished nutritive condition is expected to increase tissue pollutant levels. Exposure to outdoor conditions will work in the opposite direction. Incidence of disease may handicap the ability of an individual to excrete pollutants. The effect of a biased age-composition of the sample or sex ratio may operate in any direction. It is clear that this makes samples from strandings difficult to work with, and ones from which spurious conclusions can be easily drawn.

Fig. 6 shows the frequency distributions of PCB concentrations in Mediterranean striped dolphins found washed ashore and in free-ranging individuals sampled using biopsy techniques, and therefore considered to be more representative of the actual population. Both samples were collected during the same time period (1987-1994) and region (northeastern coast of Spain). Stranded individuals affected by the Mediterranean morbillivirus epizootic were not included in this sample, nor were biopsies from free-ranging dolphins collected in 1990, the year when the event affected the sampling area. As can be seen, concentrations found in dolphins sampled with the biopsy dart (with the exception of a single individual that carried abnormally high concentrations), follow quite closely a normal distribution. The concentrations found in stranded dolphins, in contrast, exhibit a more irregular distribution, with more extreme values, both above and below the majority of the live, free-ranging population. The reasons for this are unclear, although it is likely that undernourished individuals comprise the most highly polluted component of the stranding sample, while individuals with long post-mortem times comprise the less polluted one. In conclusion, a stranded sample is considered to be a poor representation of the true population, particularly if the sample size was small and is therefore likely to produce biased results.

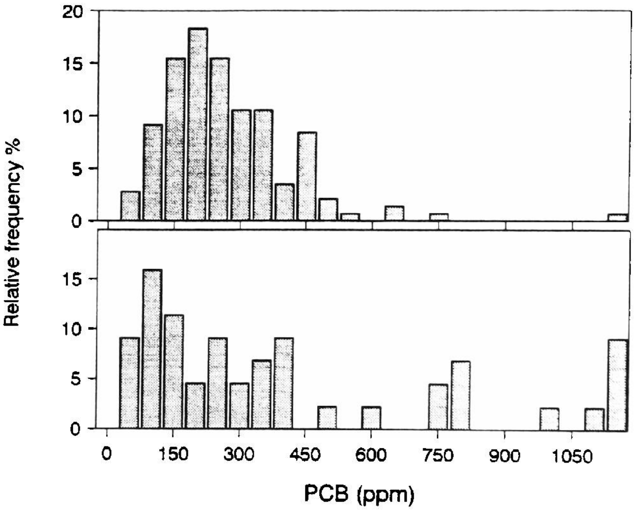

Fig. 6. Frequency distributions of PCB concentrations in the blubber of free-ranging (above) and stranded (below) Mediterranean striped dolphins.

Samples obtained from whaling operations or fisheries' bycatch do not suffer from most of these drawbacks (except the potential bias in age and sex structure due to differential catchability or selection by fishermen) and are likely to be more representative of the actual population. However, relying on these operations for pollutant sampling has obvious logistical difficulties and also limits the availability of samples to a small number of species and geographical regions.

Collection of biopsies from free-ranging cetaceans appears to be a practical alternative and many researchers have shifted to this technique in recent years (Aguilar and Borrell, 1994b). Biopsies can be collected from a reasonable number of individuals, the tissues obtained are fresh, samples can be considered to be a reasonable representation of the population and the collection technique is essentially unharmful to the sampled individual. However, the technique does have a number of limitations. Currently-used biopsy darts are only capable of extracting skin and the superficial layers of the blubber. In large cetaceans these superficial layers are mostly devoted to thermoregulation, so the sample collected may not be fully representative of the body load of certain lipophilic pollutants (Aguilar and Borrell, 1991). This limitation may be solved using a dart capable of penetrating the whole blubber thickness in order to collect a sample containing a full representation of the blubber strata (Lambertsen *et al.*, 1994), but this type of dart is obviously more invasive than those acting only at the superficial layers.

An important limitation is that, because samples are collected from free-ranging individuals, no information is usually available on their main biological characters, many of which are relevant to a proper evaluation of the levels of pollutants present in the tissues. However, recent developments have solved some of these limitations. Body size can be measured by photogrammetric techniques, e.g. gender determined using a number of techniques based on DNA analysis (e.g. Baker *et al.*, 1991; Palsbøll *et al.*, 1992) and nutritive condition assessed through the richness in triglycerides of the blubber layer (Aguilar and Borrell, 1990). It is likely that in the near future it will be possible to determine reproductive condition of individuals by analysing the hormone content of blubber, but we lack methods to determine other key factors affecting pollutant tissue levels, such as age.

Interpretation of tissue levels and loads

The patterns described above are reasonably consistent across many species and populations. However, deviations are not exceptional and researchers should be aware that substantial variation occurs among species, populations or even population components.

A paradigmatic example is the sperm whale, as the sexes distribute differently. Females of all ages and juveniles inhabit tropical and temperate waters throughout the year and comprise the so-called 'nursery' schools (Best *et al.*, 1984). Some large males move into these schools for undetermined periods of time, but for much of the time adult males move to cooler waters. This segregation implies a substantial difference in the diet, on the pollutant profile and the content of the food resources on which the different population components feed. In addition, adult males are capable of undertaking much longer and deeper dives, and consume prey located at different depths than those typical of females and juveniles. This difference in diet occurs even when both sexes share geographically identical feeding grounds. The size of the consumed prey is also highly variable, being much larger in adult males than in females or juveniles of either sex (see a review of sperm whale feeding in Clarke, 1980). Further, males show a strong tendency to take other prey than squid, whereas females seem to be much more dependent on cephalopoda. Besides these differences in feeding regime, the species is highly dimorphic and the body mass of adult males is about 3-4 times that of adult females. Since adult males inhabit colder waters and are subject to strict and more energy-demanding migratory regimes, the relative contribution of blubber to body mass is about 25%, as compared to 18-20% in females (Mizue, 1951; Best *et al.*, 1984; Evans, 1987).

These differences among sexes or age-classes obviously have an impact on the pollutant concentrations that sperm whales carry in their tissues. In effect, they follow none of the patterns of variation described above. Levels in females are higher and different in profile than males, and age-related variation in males is non-existent; a decrease in levels has even been suggested for at least the first quarter of the lifespan (Aguilar, 1983; Henry and Best, 1983).

Sperm whales are perhaps a remarkable example of complexity with regards to population biology among cetaceans, but sex- or age-related variation in diet, daily food intake rate, body size, body composition, or behaviour, are frequent among cetaceans and should be carefully considered when interpreting pollutant loads.

Toxicological implications of individual variability in pollutant levels

The toxicological implications of the age-related patterns observed for most pollutants are not obvious. While it is true that pollutant levels are usually low in young animals and high in adults, their actual impact on the individual is not necessary proportionate. Neonates and calves exhibit greater sensitivity than adults to certain toxicants, particularly carcinogens. For example, polycyclic aromatic hydrocarbons do not usually induce liver cancer in adult laboratory animals, but do so when administered to newborns because of the rapid growth of their liver. Furthermore, at advanced ages, the biotransformation capacity of hepatic microsomes weakens and many biochemical and physiological functions such as renal and hepatic blood flows or the efficiency of the urinary and biliary excretory systems decrease; thus older animals may have an increased tissue sensitivity to some toxins (Sipes and Gandolfi, 1991; Williams and Weisburger, 1991).

These changes associated with ageing point to a relatively higher sensitivity to xenobiotics in both the young and the old. However, the ability to biodegrade compounds is not necessarily a recipe for minimising their effect (Reijnders, 1994; Reijnders and de Ruiter-Dijkman, 1995). Some pollutants, such as certain PCB congeners, DDT or lead, generate degraded or biotransformed forms that are more toxic than their respective parent compounds. Moreover, certain chemicals, (e.g. carbon tetrachloride) are inactive in their original form and require biotransformation to exert their toxic effect. In these cases, sensitivity to the agent will follow a reverse trend and exposure to the chemical is expected to be less hazardous in both younger and older animals.

Gender also plays a key role in the detoxification process. As seen above, the enzyme system of males is better equipped to cope with xenobiotics than that of females, so the capacity to degrade foreign chemicals is higher in males. This difference appears to be linked to the balance of sex hormones, and artificial alteration of this balance in laboratory animals results in biotransformation rates of females approaching those observed in males, and vice versa. However, this potential response in males should not be taken as direct evidence that they are less susceptible to the toxic impact of chemicals than females. Indeed, if the toxic effect is produced by a metabolite or reactive intermediate instead of the parent compound, males will show a greater susceptibility to the agent. For example, male rats are more likely to suffer hepatic injury by carbon tetrachloride than females because, in the latter, degradation and subsequent formation of toxic forms is a lower process (Sipes and Gandolfi, 1991).

In summary, it is important to remember that, as when interpreting tissue pollutant levels, a toxicological evaluation should only be attempted when taking into account the available knowledge on the biology of the species, and of the population, population component or individual subject to study.

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