their acyl-free moieties, as well as two sphingolipids, is reviewed.

Wax Esters: Major Marine Metabolic Energy Sources

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The importance of polyunsaturated wax esters as metabolic reserves in marine copepods has been recognized by Lee *et al.* (1970). These major zooplankton of the world's oceans convert the highly unsaturated triglycerides of diatom and dinoflagellate algae on which they graze into wax esters comprised of polyunsaturated fatty alcohols and polyunsaturated fatty acids. Metabolic-turnover experiments have revealed that the animals first utilized the triglyceride components of their stored lipids and then more slowly metabolized their wax ester reserves. Although all copepods store wax ester, those of temperate and polar waters have adapted to their environment and long unproductive winters by accumulating up to 75% of their body weight as wax ester. In warm tropical waters the continuity of the food supply makes long-term energy supplies unnecessary and wax ester storage is minimal.

Wax ester accumulation and metabolism in marine animals appears to be controlled through wax lipase. Stage V copepodites, immediate precursors of the egg-bearing adults, must store energy reserves for winter 'hibernation', moulting, mating and egg production. At this stage they lack wax lipase activity, although triglyceride lipase is relatively active. Stage V copepodites of *Calanus plumchrus* contain up to 60% lipid, which is comprised of 90% wax ester. After starvation for 50 days their triglyceride content diminished to zero. *Gaussia princeps* lipid composition changed from 49% wax ester and 18% triglyceride to 61% wax ester and 2% triglyceride during 5 days' starvation (Lee *et al.*, 1972).

Anchovies, herring, sardines and salmon, all predators on wax-rich animals, possess active wax lipases that cleave the wax esters quickly, leaving no trace of wax ester in serum lipoproteins. Wax digestion in fishes occurs in the mucosa of the pyloric caecum. Wax globules are adsorbed in the folds of mucosal surfaces. Blood serum of young salmon feeding on a high-wax diet is rich in triglyceride and cholesteryl ester and contains no wax ester. The site of fatty alcohol oxidation lies in the intestinal mucosa. A mechanism for conversion into fatty acyl ester involving membrane-bound ether and plasmalogen intermediates appears probable.

The copepod wax esters are among the most un-

saturated lipids in Nature, being derived from algal triglycerides containing $C_{22:6}$, $C_{20:5}$ and $C_{20:6}$ fatty acids. The fatty alcohol moiety is relatively unsaturated, 13% $C_{16:0}$, 18% $C_{20:1}$, 41% $C_{20:4}$ and 8% $C_{22:6}$ alcohol in *Calanus helgolandicus* (Lee *et al.*, 1971). Carnivorous deep-sea copepods contain up to 50% of $C_{16:0}$ alcohol, reflecting their dietary differences. The fatty acids of the wax esters of near-surface herbivorous copepods are less saturated than the alcohol moieties. They included 23% $C_{20:5}$ and 14% $C_{20:4}$ fatty acids in *Calanus hyperboreus*. It is observed that surface-feeding copepod species in temperate and polar waters store their highly unsaturated wax ester in a very large abdominal oil sac, whereas the bathypelagic animals of the deep sea, living at temperatures near 0°C, store relatively saturated wax esters. This is contrary to the usual variation in unsaturation with depth. These animals store their lipid in dispersed globules throughout their tissues. It is presumed that this is an evolutionary adaptation to facilitate utilization of the more saturated wax esters at the lower temperatures.

Wax esters and triglycerides exhibit different densities and compressibilities relative to that of sea water. We have isolated both in large quantities for measurement of their physical properties. The important vertical-migrating animals of the sea have selected wax ester for buoyancy regulation. All animals living below 700m have been observed to contain wax ester (Lee *et al.*, 1972). The most numerous fishes of the seas, the bristlemouth (cyclothone) fishes, Gonostomatidae and the lantern fish, Myctophidae, contain 53% wax ester in their lipids; the coelacanth contains 70% wax ester (Nevenzel, 1970). All members of bathypelagic food chains contained large amounts of lipid rich in wax ester. The utilization of lipid in the marine environment, like that in desert animals without available fresh water, allows extensive production of metabolic water. By selection of wax esters in addition to triglyceride, certain marine animals are able to exert added control over their lipid metabolism and to migrate vertically with less expenditure of energy. Wax ester accumulation appears to have been an important evolutionary adaptation.

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