I. Introduction

The hypothesis that thyroid function in fish may be altered by photoperiod arose, in part, from observations of seasonal changes in thyroid activity. Cyclic changes in thyroid function follow a variety of patterns in teleosts, and they remain generally poorly understood in terms of how they are regulated and what physiological purposes they serve. In some instances, seasonal alterations in thyroid function coincide with sexual development or temperature changes, but in others it appears that photoperiod could be the primary environmental cue for thyroid seasonality. Correlative changes alone only indirectly infer cause-and-effect relationships, however, and controlled experiments have been required in order to establish the specific environmental variables that govern thyroid function. Experimentation with fish maintained on controlled lighting has shown that a change in daylength alone can have profound effects on thyroid function in teleosts, although it has become abundantly clear that temperature and other factors are also important. Species differences appear to be the rule rather than the exception.

There are also reports of diurnal rhythms in thyroid activity in a few teleost species, although it is not yet known how prevalent these cycles are or what regulates them. The superimposition of daily rhythms on seasonal rhythms could conceivably account for some of the complicated patterns of thyroid activity that have been observed. Compounded rhythms of this sort may modulate the production and peripheral actions of prolactin in teleosts (Sage and deVlaming 1975). At this time, however, it would be unwise to assume that diurnal thyroid cycles are ubiquitous among teleosts.

In this report, seasonal and diurnal cycles in thyroid function in teleost fish are examined as they may relate to photoperiodic control mechanisms. The interpretation of the biological significance of these cycles is limited by the plentiful gaps and contradictions in the literature on physiological roles of thyroid hormones in fish. The experimental evidence implicating photoperiodic regu-
lation of thyroid activity in fish is summarized, and one means by which this environmental variable could exert influences at the level of the thyroid follicles is also considered.

II. Seasonal Changes in Thyroid Function

Eales (1979), in his comprehensive review of thyroid function in fish, pointed out that although seasonal changes in thyroid activity have been documented in more than 20 teleost species, few if any sweeping generalizations could safely be made. One recurring theme in this body of literature is a spring or summer peak in thyroid activity followed by late-summer quiescence, but Eales (1979) noted that these seasonal patterns appeared to be complicated by the simultaneous effects of temperature, photoperiod, and certain kinds of physiological changes.

In the earliest of investigations of thyroid seasonality in fish, qualitative differences in the histological appearances of thyroid follicles were described. Citing changes in the size and shape of thyroid follicular epithelial cells and in the appearance of colloid in Atlantic salmon, *Salmo salar*, Hoar (1939) concluded that increased glandular activity was evident in spring, with signs of moderate activity in summer and minimal activity in winter. This pattern was comparable to those previously found in the loach, *Misgurnus fossilis*, by Lieber (1936) and in the eel, *Anguilla vulgaris*, by von Hagen (1936). The agreement among these studies and earlier work on amphibians and reptiles led Hoar (1939) to summarize that thyroid function in ectotherms is not directly related to temperature as it is (inversely) in homeotherms.

Barrington and Matty (1955) described the consistent effects of thyrotropin treatment on thyroid follicular epithelial cell height and applied this quantitative technique to the study of thyroid seasonality in *Phoxinus phoxinus*. The peak in epithelial cell height in this minnow occurred in February, although a rather sparse sampling protocol was used. It was determined experimentally that thyroid epithelial cell height was positively correlated with temperature under conditions that included constant darkness, suggesting to these authors that the midwinter activation of the thyroid took place despite a presumably inhibitory effect of low temperatures (Barrington and Matty 1955). Similar histological cyclicity was discovered in the epithelial cell height measurements of both immature and adult cod (Woodhead 1959). These results were in direct contrast to the earlier reports, and they set a precedent by (1) establishing the need to consider species differences in thyroid seasonality and (2) raising the possibility of environmental variables other than temperature in the regulation of these cycles.

A new dimension in the analysis of thyroid activity was added with the advent of radiochemical methods, which have been used widely in studies of thyroid function in fish since the mid-1950s. Iodine-131 uptake was found to vary seasonally in *Fundulus heteroclitus*, with maximal uptake in January, although this