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19. The internal probe was end-labeled in the presence of [$^{32}$P]ATP (3000 Ci/mmol) by T4 polynucleotide kinase (*10*). The probe hybridization was carried out at 42°C in 6× SSC, 0.1% SDS, 0.1% sodium pyrophosphate, 0.1% Denhardt's solution, 50 m*M* tris-HCl, *p*H 7.5, and 50 μg/ml denatured herring sperm DNA. The blot was washed in 2× SSC, 0.1% SDS at 42°C.
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# Aquatic Productivity and the Evolution of Diadromous Fish Migration

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**Diadromous migration, in which some fish species migrate from freshwater and feed in the ocean (anadromous species) and others migrate from the ocean and feed in freshwater (catadromous), has long been perplexing. However, when the distribution of diadromous species is examined with respect to global patterns in aquatic productivity, this apparent paradox is resolved. The contrasting directions of migration can largely be explained by the relative availability of food resources in ocean and freshwater habitats. Oceans are more productive than freshwaters in temperate latitudes, and anadromous species predominate. In contrast, catadromous species generally occur in tropical latitudes where freshwater productivity exceeds that of the ocean.**

LARGE-SCALE MOVEMENTS OF ANIMALS are found in many taxonomic groups (*1*). The migrations of diadromous fish species, those that migrate between the ocean and freshwater, are particularly enigmatic because this behavior necessitates physiological changes in osmoregulation (*2*). Diadromous fishes are found in 28 families and include two distinctly different groups: (i) 87 anadromous species, such as salmon (Salmonidae) and lamprey (Petromyzontidae), which are born in freshwater, migrate to the ocean, and return to freshwater to spawn; and (ii) 41 catadromous species, such as some eels (Anguillidae) and mullets (Mugilidae), which are born in the ocean, migrate to freshwater, and return to the ocean to spawn (*3*). The existence of these contrasting directions of migration has long been perplexing. Indeed, it has been described as a paradox in animal migration (*1*). We report that diadromous migrations may occur in fishes because of the differential availability of food resources in ocean and freshwater habitats. Moreover, it is because the relative productivity of oceans and freshwaters is not constant but changes with latitude that the contrasting directions of anadromous and catadromous migration can exist.

In theory (*4*), diadromous life histories will evolve through natural selection only when migration across the ocean-freshwater boundary provides a gain to individual fitness (lifetime reproductive success) that exceeds the costs of this behavior. These costs may include adjustments to physiology, allocation of energy for swimming, and increased probability of mortality during migration. Several authors (*1, 5–9*) have speculated on what factors might favor juvenile fishes deserting their habitat of birth for residency elsewhere. Among these have been decreased predation, decreased disease, decreased physiological stress, or increased food availability. To date, these hypotheses have not been tested quantitatively because of the logistic problems presented by animals that may travel several thousand kilometers and because of our limited knowledge of the life histories of many fish species.

McDowall's (*3*) findings on the global geographic distribution of diadromous species are shown in Fig. 1A. These data indicate latitudinal differences in the worldwide distribution of anadromous and catadromous fishes, with anadromy being more common in temperate (including arctic) latitudes and catadromy in the tropics. Therefore, any hypothesis for the evolution of diadromy must not only provide evidence for a substantial fitness benefit to a diadromous migrant, but must also account for the geographical distribution of diadromy. A hypothesis based on the differential availability of food in the oceans and freshwaters meets these criteria.

Let us first consider whether such a hypothesis can allow for significant fitness benefits through migration. The importance of food intake for body growth (*10*) and the contribution of growth to fitness through decreased mortality (*11*), increased fecundity (*12*), and improved male (*13*) and female (*14*) breeding success have been documented in many fishes. There are also well-studied cases of growth rates increasing with movement across the freshwater-ocean boundary. Juvenile anadromous Pacific salmon, for example, can experience a 10 to 50% increase in their daily growth rate during their first week of ocean life (*11*). In addition, a recent survey by Gross (*4*) of diadromous and nondiadromous populations within seven salmonid species showed that the only significant difference in major life history traits was that individuals in

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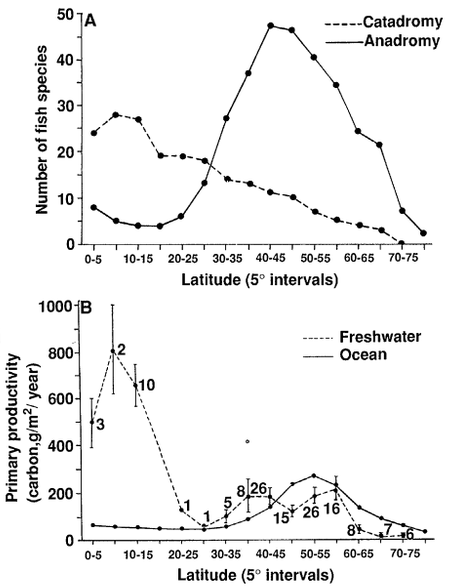


**Fig. 1.** (**A**) The number of anadromous and catadromous fish species found in each 5° interval of latitude, averaged from both Northern and Southern hemispheres. We reanalyzed McDowall's (*3*) data on the latitudinal ranges of all known diadromous fishes and calculated the number of anadromous or catadromous species found within each 5° interval. As such, wide-ranging species will be counted in more than one latitudinal interval. (**B**) Annual primary productivity, measured in grams of carbon fixed per square meter per year, of freshwater and ocean habitats with latitude. The most complete sets of productivity data that allow comparison of freshwaters are by Burgis and Dunn (*16*), Brylinsky (*18*), Westlake *et al.* (*17*), Wetzel (*19*), and Kahn (*20*). These sources provided annual primary productivity data for 135 freshwater bodies which we grouped into intervals of 5° latitude. Following Brylinsky we combined data from the Northern and Southern hemispheres because of a paucity of data in some latitudes. Plotted are the mean ± 1 SEM; sample sizes are shown. There were no data for the 15° to 20° or 75° to 80° latitudinal ranges. Note that we excluded an extreme productivity value [for Red Rock Tarn, 2200 g of carbon per square meter per year (*20*)] because it is nearly four times the next largest value in that latitudinal range ($n$ = 9, range 24 to 614 g $m^{-2}$ $year^{-1}$). The open circle indicates where the mean would have fallen had the point been included. Marine productivity is from Bunt (*21*, figure 8-1) who divides the world's ocean waters into five productivity categories (0–50, 50–100, 100–200, 200–400 and >400 g $m^{-2}$ $year^{-1}$). We calculated the productivity for each 5° of latitude by multiplying the number of points of each productivity category by the average value of that category, that is, 25, 75, 150, and 300 g $m^{-2}$ $year^{-1}$ (we used 400 g $m^{-2}$ $year^{-1}$ as a conservative value for the over 400 category). We combined the data from both the Northern and Southern hemispheres to be comparable with the freshwater data (the ocean values for the Northern and Southern hemispheres showed similar trends with latitude and were highly correlated when values equidistant from the equator were plotted against each other; $r^2$ = 0.81, df = 93, $P < 0.001$). The 58,129 values taken from Bunt's map produced an average of 3,633 points per 5° interval (SEM = 211, range 1,869 to 4,660). Only the means are plotted; error bars are too small to illustrate.

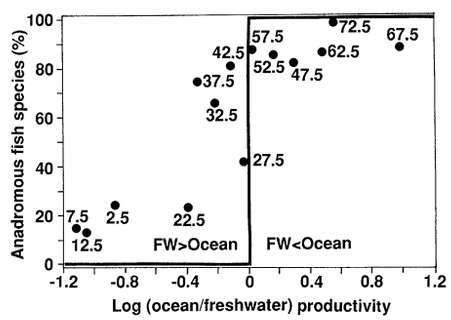


**Fig. 2.** The relation between relative productivity of the world's oceans and freshwaters and the proportion of diadromous fishes that are anadromous. The data from Fig. 1B were converted to the $\log_{10}$ of ocean productivity divided by freshwater (FW) productivity in grams of carbon per square meter per year. These calculations were made for each 5° of latitude and thus approximate neighboring oceans and freshwaters. Log(ocean to freshwater) productivity is zero when the productivity of neighboring oceans and freshwaters is equivalent. The heavy bar is the theoretically predicted frequency of anadromy. The productivity of freshwater is greater than productivity in the ocean to the left of the vertical bar, and conversely the ocean productivity is greater than freshwater on the right. The latitude for each point is shown.

diadromous populations produced more eggs than those in nondiadromous populations as a consequence of the former's larger body size. Finally, an experimental increase in the availability of freshwater food was found to decrease the incidence of anadromous migration by arctic char (*Salvelinus alpinus*) (*15*). These studies indicate that access to food resources for body growth is an important benefit from diadromy.

We tested the ability of the food availability hypothesis to predict direction of migration by comparing the direction of diadromous movement with the relative availability of food. This hypothesis predicts that anadromy will be more likely to evolve when ocean productivity is greater than that in neighboring freshwaters; catadromy will evolve when freshwater food productivity exceeds that of the ocean. As an estimate of food productivity in different biomes we employed annual primary productivity data. Measured in grams of carbon fixed per square meter per year, primary productivity is probably well correlated to food availability for many planktivorous fishes and indirectly correlated for piscivorous or macrophagus species (*16*).

Primary productivity data for oceans and freshwaters throughout the world (Fig. 1B) show a sharp peak in freshwater productivity relative to marine waters in tropical latitudes; marine productivity significantly exceeds that of freshwater in temperate and polar latitudes. Although primary productivity is known to be influenced by many variables, including temperature, solar radiation, currents, upwellings, and nutrient supply (*17–21*), the basis for this pattern shown in Fig. 1B is not well understood (*17*). Such a pattern in aquatic productivity does suggest, however, that some fishes in temperate latitudes may experience greater foraging opportunities in the oceans than in freshwaters, whereas certain fishes in tropical latitudes have greater foraging opportunities in freshwater habitats. When we reexamine McDowall's data on the direction of diadromy in conjunction with our data on patterns of primary productivity (Fig. 1, A and B), we see that migration to freshwater (catadromy) is more frequent in tropical latitudes, where freshwater productivity is greater than that of oceans. Similarly, migration to the oceans (anadromy) is more frequent in temperate latitudes, where ocean productivity is greater than that in freshwater.

We can refine our test by examining only those fish species that are known to be able to migrate and predicting their direction of diadromy. By comparing relative productivity against the direction of diadromous migration, we focus attention on the relation between food and migration behavior. Where the ocean is more productive than neighboring freshwater, diadromous fishes should be anadromous; and where freshwater is more productive than the neighboring ocean, diadromous fishes should be catadromous.

The observed frequencies of anadromy and catadromy follow the prediction (Fig. 2): where the productivity of the ocean exceeds that of neighboring freshwaters, as much as 100% of diadromous fishes are anadromous. Conversely, where freshwater productivity exceeds that of neighboring oceans, catadromy is the dominant form of diadromy. Where neighboring oceans and freshwaters are similar in productivity, a threshold exists in the relative frequency of anadromy and catadromy. Thus, the differential productivity of aquatic habitats appears to explain the contrasting directions of diadromous migration in fishes.

The hypothesized relation between aquatic productivity and the direction of diadromous migration is evident in spite of several complicating factors. For instance, primary productivity is imperfectly correlated with food availability for species feeding at higher levels of the food chain (*16*). Second, our analysis overlooks the fact that some species

move north or south after crossing the ocean-freshwater boundary [for example, some anadromous salmon leaving the Fraser River, British Columbia, eventually move 5° to 15° north in the ocean (*22*)]. Third, selection for migration will also be affected by other factors (*1*), including the presence of competitors in a habitat, which influence food abundance, and predators and disease, which affect survivorship. These factors are not considered in our analysis because of the lack of such data for each latitude. However, it would be of interest to investigate the significance of these factors in explaining the variation in Fig. 2. The remaining paradox, that in some waters both anadromous and catadromous species co-exist (*1*), may require survivorship data or more detailed foraging data.

In spite of these potentially complicating factors, the food availability hypothesis appears to be consistent with the global geographic pattern of diadromy in fishes. We therefore conclude that food availability is an important factor in explaining not only where diadromous fishes occur, but also why fish migrate across the ocean-freshwater boundary, as well as their direction of movement.


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# Nicotinic Antagonists Enhance Process Outgrowth by Rat Retinal Ganglion Cells in Culture


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**Functional nicotinic cholinergic receptors are found on mammalian retinal ganglion cell neurons in culture. The neurotransmitter acetylcholine (ACh) can be detected in the medium of many of these retinal cultures, after release presumably from the choline acetyltransferase–positive amacrine cells. The postsynaptic effect of endogenous or applied ACh on the ganglion cells can be blocked with specific nicotinic antagonists. Here it is shown that within 24 hours of producing such a pharmacologic blockade, the retinal ganglion cells begin to sprout or regenerate neuronal processes. Thus, the growth-enhancing effect of nicotinic antagonists may be due to the removal of inhibition to growth by tonic levels of ACh present in the culture medium. Since there is a spontaneous leak of ACh in the intact retina, the effects of nicotinic cholinergic drugs on process outgrowth in culture may reflect a normal control mechanism for growth or regeneration of retinal ganglion cell processes that is exerted by ACh in vivo.**


NICOTINIC CHOLINERGIC DRUGS have long been studied for their role in synaptic transmission in the nervous system. Besides their function in intercellular communication, trophic effects of acetylcholine (ACh) and other presumptive neurotransmitters have been postulated in the mammalian central nervous system. For example, the activation of ACh, norepinephrine, and *N*-methyl-D-aspartate (NMDA) receptors appears to facilitate the synaptic plasticity that affects ocular dominance columns after monocular visual deprivation (*1*). Factors that inhibit neuronal growth have often been associated with glial cells (*2*). Recently, however, in invertebrate and submammalian vertebrate nervous systems, growth-inhibiting properties have been attributed to classical neurotransmitters (*3*). Hence, neuronal interactions, possibly mediated by neurotransmitters, may be important determinants of the cytoarchitecture of the central nervous system (*4*).

In some cell culture systems neurotransmitters leak into the culture medium (*5*), and spontaneous release of ACh occurs in retinal cultures such as those described here (*6*). This release of ACh resembles at least to some degree a naturally occurring event in the intact retina (*7*). Thus, in tissue culture it may be possible to investigate the chemical nature of neuronal interactions associated with cell growth in a precisely controlled environment.

In the present study we used cultures of postnatal rat retinal cells because they provide a system in which neurite outgrowth can be monitored from an identified central neuron, the retinal ganglion cell (*8, 9*). We found that the addition of nicotinic antagonists to the culture medium for the first 24 hours after plating resulted in a striking increase in process outgrowth by the ganglion cells. During the same period, there was no effect of nicotinic antagonists on the survival of the ganglion cells compared to controls, suggesting that the effect was in some way specific for the growth of neurites and not merely influencing the overall health and welfare of the cells.

Retinal cultures were produced as described previously from 7- to 12-day-old rat pups (*8*) and grown in a specific batch of rat serum; under these conditions the culture fluid was found to have endogenous levels


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