obtain in the *Drosophila* populations, which therefore cannot be said to belong to different ecological niches according to that standard. If the ecological niche of a species is taken to include all the essential components, both physical and biotic, of the environment in which the species lives, then *D. pseudoobscura* and *D. serrata* have different ecological niches. But so do any two species, whether they coexist or not in their natural habitats, and whether they coexist or not in an experimental microcosm.

One serious difficulty that has plagued the controversy around the principle of competitive exclusion is that the terms "competition" and/or "ecological niche" are frequently used without adequately defining them.

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Timing of the Appalachian/Caledonian Orogen Contraction

LOWER Palaeozoic faunal "provinces" in the northern hemisphere were controlled principally by the Appalachian/Caledonian orogen. Tuzo Wilson postulated a proto-Atlantic ocean closing during the Lower Palaeozoic so that the "American" and "European" landmasses collided during the Middle Palaeozoic[1]. Dewey remarked that faunas were of great potential value for timing this contraction, which in his model finished during the Devonian[2]. There is a differentiation of invertebrates into two or more markedly distinct faunas in the early Ordovician, which later merged[3]. This Wilson and Dewey related to closure along the length of the orogen.

After studying the widespread agnathan fish known as thelodonts, I think a more precise timing of events is possible. These mobile fish lived in marine offshore environments during the Silurian, and were tolerant of changes in salinity, evolving by Dittonian times into freshwater fish.

There are two separate Silurian thelodont faunas in Britain. That of the Scottish Inliers and Pentland Hills is well known: *Thelodus scoticus* from the lower fish band and *Thelodus taiti* and the spiny *Lanarkia* species from the upper This fauna is almost identical to that found at Ringerike near Oslo but is not known elsewhere[4].

The Anglo-Welsh shelf sequence yields abundant isolated scales of predominantly *Thelodus parvidens* and *Logania ludlowiensis*, essentially the same as from the German Beyrichienkalk[5], Ramsåsa, Gotland, Estonian Saaremaa (Oesel Island) and to the west in New Brunswick. One anomaly, *Phlebolepis*, only found on Oesel in the southern province, is now being found in the Canadian Arctic islands[6]. This is the only evidence of access for a migration from north to south.

Clearly a barrier isolated Scotland and Norway from other regions. They were apparently part of a north landmass cut off by a substantial barrier to migration, be it true ocean or the effect of a strong current system in the Caledonian channel.

By Downtonian times there was a shift to more brackish environments in Britain[7]. The thelodont assemblages remain basically unchanged until late Downtonian when new faunas take over in freshwater environments, characterized by the incoming traquairaspids[8] and the ubiquitous thelodont *Turinia pagei*. This is found in the Anglo-Welsh basin, Scotland, the Baltic and Beyrichienkalk, Russia and Vestspitsbergen. It should turn up in all Dittonian fluviatile sediments, aided by a marine larval dispersal phase in its life cycle. This does help to pinpoint the ending of Dewey's zone E during the Downtonian. Britain was at the meeting point for migration before this time. The principal changes during late Silurian times resulted in the disappearance of the barrier and more cosmopolitan faunas.

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Protogynous Sex Reversal in the Fish *Anthias squamipinnis* (Teleostei, Anthiidae) regulated by the Presence or Absence of a Male Fish

PROTOGYNOUS or protandrous hermaphroditism among teleost fishes has often been described[1]. Although found in various families, the phenomenon is especially common among Serranidae and closely related groups. It was briefly mentioned for the Mediterranean *Anthias anthias*[2,3]. While working on the ecology and reproductive behaviour of the Red Sea fish *Anthias squamipinnis*, D. Popper and I (unpublished results) found protogynous hermaphroditism and intersexuality in this species which was confirmed by N. Gunderman and me (unpublished results) when we observed changes in the gonads[4]. To establish whether environmental factors regulate this sex reversal, or if it is a continuous and non-predictable process, I carried out a series of experiments with *Anthias* performed in captivity during 1968 and 1969. When ten to twenty females and one or two males were kept together for several months there was no change in morphology or behaviour to indicate sex change, although cut sections of these fishes revealed advanced degeneration of the ovaries.

When groups of twenty females were isolated from males one of the females changed to a male after 2 weeks, developing the typical colour pattern and behaviour of the male. If this male were removed then a new male gradually developed from among the nineteen remaining females. By continuously repeating this process, twenty males had been developed from the original twenty females by the end of the year.

We can now regulate the sex reversal of groups of females by including or excluding a male in the aquaria. Even when the males were behind an isolating glass, there was no sex change among the females. In nature along the littoral of the Gulfs of Aqaba and Suez, *A. squamipinnis* occurs in stationary groups of hundreds or thousands on isolated blocks of coral. Such a population normally consists of 80–90 per cent swarming sub-adult and adult females and a few active, territorial males, spread along the top of the coral rock.

Such a group of *Anthias* seems to form an ecological unit in which the "flow" of sex inversion is in some way controlled by the numbers of males. From the point of view of survival, such an arrangement is of obvious value. Because the males are only "produced" if there is a need for them—that is, if their density decreases—the population usually consists largely of reproducing females. Because the eggs and larvae of this species are pelagic,