CAN THEORIES OF "MATCH" SITUATIONS IN HIGH PRODUCTIVITY FRONTAL AREAS BE APPLIED TO REARING OF MURICIDS?

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INTRODUCTION

Most pelagic as well as benthic organisms produce planktonic eggs and larvae. Early in life these larvae share similar ecological niches and live under the same set of "rules of life". Consequently many of the species specific characteristics and adaptations that separate species in adult life will not apply in larval life and discussions of ecological aspects concerning these organisms can be made for larvae in general, even though the different species later in life have very different ecological positions.

Fish spawning patterns

Many fish species in temperate waters have species specific patterns of migration (Harden Jones, 1968) (Fig. 1). Generally the adult fish stock migrates against current (contranatant migration) from its feeding area to the spawning area.

After spawning the adults return to their feeding ground down current (denatant migration). This migration may be repeated by the adult fish every year, many times through their lifetime.

The newly spawned fish larvae are planktonic organisms and will drift passively with the prevailing currents, which under favorable conditions transports them to the nursery areas, where they will gain further size and finally recruit to the adult stock. The migration from the spawning area through the nursery area to the adult stock takes place only once in a lifetime, and fish that reach the nursery areas have gained so much size that their chance of survival and recruitment to the adult stock is relatively large.

The planktonic larvae that drift from the spawning areas are very small (only a few mm) and have tremendous mortality rates, typically around 10% per day, but much higher mortalities per day have been reported (Cushing, 1974). These high mortality rates are balanced by millions of eggs spawned per individual by the species with pelagic, planktonic larvae.

Size and mortality rates

Mortality rates of marine pelagic organisms are correlated with age and size of the organisms (Cushing, 1974, 1975; Purcell et al., 1990).

Many fish species increase their weight by more than 6 orders of magnitude from newly hatched larvae to adults. During this period of growth they encounter a range of different predators largely determined by a general predator-prey size relation. Predators which are active hunters, snapping prey, for example fish, are 10 to 100 times larger (length) than their prey. Predators with a filter feeding mechanism, for example mussels or whales feeding on krill may be several orders of magnitude larger.

As the number of potential predators decreases when the prey organisms increase their size, mortality decreases as a function of the age of the prey organism (Pearcy, 1962).
Figure 1. The triangle of fish migration. A; Spawning area. B; Nursery area. C; Adult stock. The larvae move from the spawning area to the nursery area as planktonic organisms. From the nursery area to the adult stock and from feeding grounds (C) and spawning areas migration can take place against current. (Modified from Harden Jones, 1968).

Consequently, the very early phase of larval life is an important period concerning the recruitment to the adult stock, and small changes in survival rates will dramatically affect the recruitment to the adult stocks and the fisheries.

Food may be a limiting resource and may have density dependent effects with the largest effect on the small larvae which have the highest densities.

The "match mis-match" theory

The interaction between larvae and their food has been presented in the "match mis-match" theory presented by Cushing (1973). The theory concerns the correlation in time and space between high production of food and the appearance of larvae in the water column.

Since only organisms which have survived the larval period reproduces and since the migrational species migrate back to the place where they were spawned, these species now only spawn on locations where there will be a high production of potential food organisms when the larvae appears after spawning. The survival of the larvae will depend on the production of food in these areas.

A "match" situation is characterized by the newly hatched first feeding larvae appearing in the water column in a period with high production of food in that area, and a "mis-match" situation by the larvae appearing in a period with low production of food.

In temperate waters the annual spring and autumn phytoplankton blooms are periods with high production. These blooms are caused by variations in illumination and depth of wind induced water mixing.

In the North Sea between Great Britain and Denmark the whole water column is well mixed during winter, because of high wind speed. The depth of mixing exceeds the critical depth (the depth, where respiration of the water column above equals photosynthesis (Cushing, 1973)) and production as well as standing stock of phytoplankton is low. During spring, the light intensity increases and wind speed decreases. This causes the surface water to become heated, leading to a stratification of the water column with a heated surface layer reaching down to approximately 15 m and lying on top of the colder bottom layer.

When this stratification occurs (mostly in April or May), the depth of mixing will not exceed the depth of the heated water column. As this is above the critical depth, photosynthesis in the surface layers exceeds respiration leading to an increased primary production and a high standing stock. As there is no nutrient influx to the surface waters, nutrient limitations will after a short time limit production and because the algae sink out of the photic zone, production and standing stock decrease.

The autumn phytoplankton bloom takes place in September and October and is caused by
the mixing of the water masses as a result of the increased wind force and decreased illumination of the water surface.

The energy of the two phytoplankton blooms in the North Sea area is transferred into herbivores. The standing stock of zooplankton is small in early spring and consequently a large amount of the produced biomass during this bloom will be lost from the photic zone and will instead benefit the benthic system (Graff et al., 1983; Graf, 1987), whereas most of the energy accumulated during the autumn bloom will be used by the pelagic herbivores.

Cushing (1973) has compared the spawning time of herring (Clupea harengus) and the standing stock of algae in the North Sea area east of the British Isles. There are a number of discrete stocks of herring in the North Sea area with different spawning times through out the year.

The autumn spawning herring on the North-east coast of Scotland i.e. the Buchan area, spawns during the autumn phytoplankton bloom maybe because this is a period with high production.

In the northern part of the North Sea the spring spawning herring spawns in a period with high primary production, and the standing stock of algae is higher during the spring phytoplankton bloom than during the the autumn bloom in this area.

These are examples of potential "match" situations. In the English Channel the herring stock spawns during winter in a period with very low primary production, and there seems to be no "match" in this case.

Frontal systems - local high productivity areas.

There may be many other factors involved in these very general considerations and the conclusions are rather speculative.

Figure 2. Distribution of temperature and zonation of a thermal front. 1; Well mixed zone. 2; Stratified zone. 3; Transition zone.

In order to find more evidence concerning the larval dependence of high production of food, more narrow time intervals and smaller geographical areas must be investigated. Such smaller geographical areas have been investigated by Kiorboe et al. (1985, 1986, 1988) in the North Sea in the Buchan area and by Kiorboe & Jarnekarn (1991) in the Andaman Shelf Sea south west of Phuket Island.

The frontal system in the North Sea is a "thermal frontal system". It is a near-shore phenomenon and is created during late summer and early spring while the water column is still stratified (Kiorboe et al., 1988). Because of the very large tidal effect in this area the shallow water close to the coast is moved horizontally and the stratification is broken by turbulence and the water column is mixed.

A transect perpendicular to the coastline stretching out into the central part of the North Sea reveals 3 different water column structures (Fig. 2):
1. Near shore; a well mixed zone without stratification.
2. Far from shore, stretching to the middle of
the sea; a stratified zone with horizontal thermoclines and warm water overlying the cold bottom water.  
3. The transition zone separates 1 and 2, and the thermoclines are vertical to the bottom in this zone.

These 3 different zones are not just hydrographically different but also differ in production and food-web structures (Kiorboe et.al., 1988).

1. Turbulent, non-stratified water.

The near shore system is constantly supplied with nutrients released from the sediment by wave action, but the large amounts of inorganic seston in the water column will decrease the photic depth and light may be limiting as the depth of mixing may exceed the critical depth and the availability of nutrients may not increase production.

Different algal cells have competitive advantages in different environments and in this nutrient rich turbulent system large algal cells with high cell division rates and high V-max values are able to benefit from the nutrients available and will thereby have an advantage. They have high sinking rates and can therefore only stay in suspension in turbulent water.

Diatom cells may dominate such systems, and they also grow well when subjected to the short term fluctuations in light intensities typical of the turbulent water. Diatoms are an excellent food resource for zooplankton species, such as adult copepods because the size of the algal cells fits into the retention spectrum of the copepods. As copepod nauplii are known to be the main food source for pelagic carnivorous larvae, a high primary production of large algal cells is, in view of the very short food chain in this system, beneficial to the larvae.

2. Stratified water.

In the stratified waters far from the coast, primary production in the photic zone will be limited by nutrients because there is no input of nutrients to the system. Small algal cells are abundant in these systems. They display lower growth rates and an ability to stay in suspension by active movements via flagella.

Nano- and micro-flagellates are one to two orders of magnitude smaller than diatom cells (length). As algal cells leak metabolites to the water surrounding them (Coveney et.al., 1989), the amount leaked is proportional to the surface area. The relative leak per gram phytoplankton will be inversely proportional to the size of algal cells. Consequently the relative leak of metabolites will be largest in the stratified zone.

Bacteria are much more efficient in trapping leaked metabolites than algal cells, and a large proportion of the primary produced energy is converted into bacterial biomass.

The small algal cells do not fit into the copepod retention spectrum but ciliates will feed on these algal cells and thereby make the energy available for the copepods. This transfer of primary produced standing stock through bacteria, and organisms eating bacteria, to copepods is called the microbial loop and is known to dominate in stratified waters. As this system is not supplied with nutrients from any external source, the production is based on regeneration of nutrients in the photic zone.

3. Transition zones.

The transition zone shares some of the features of the mixed zone and the stratified zone. The algal cells will be held in the photic zone by the stratification of the water column,
and at the same time be supplied with nutrients from the mixed zone.

The de-stratification in the early autumn which leads to the autumn phytoplankton bloom is a gradual process that begins in the transition zone. In stormy periods, water is mixed in the transition zone, resulting in the transition zone moving off shore, but also supplying it with new nutrients from the underlying water. This leads to very local phytoplankton blooms. The food chain structure during these blooming periods is a combination of the food webs found in the mixed and the stratified water column (Kiorboe et.al. 1990). Both food chain structures are able to supply the copepods with food, and since studies of the functional response of copepods have shown that copepods in nature almost always are limited by food (Kiorboe et.al. 1985), they benefit from the higher standing stock of algae encountered in these transition zones. Assimilated energy is used for respiration, somatic growth and growth of reproductive tissue.

Copepod nauplii and copepodites will transfer the assimilated energy, that is not used for respiration, into somatic growth, whereas adult copepods will use it for reproduction. Consequently an increased standing stock of food will result in an increased rate of reproduction, and as the first naupliar stages serve as food for fish larvae, an increased primary production and standing stock of algae in the transition zones can benefit larvae in these zones (Berggren et.al., 1988).

Many such transition zones have been found around the British Isles, and a comparison of these transition zones with the spawning areas of herring have shown that 12 of the spawning grounds or areas with newly hatched larvae are found in transition zones (Sinclair et.al., 1985). The herring which reaches the nursery grounds on the Danish west coast in spring are spawned west of Scotland in the Buchan area. Large fluctuations in the recruitment to this stock are a well known phenomenon (Cushing, 1973).

The match mis-match theory (Cushing, 1973) would state that it is the abundance of food that governs the recruitment success as the herring carry out their denatant migration from the spawning ground to the nursery ground.

The theory presented by Sinclair et.al. (1985) stated that the thermal fronts serve as retention areas with a capability of holding the larvae back. This should maintain the discreteness of the different herring stocks, and the success or failure of recruitment should be governed by the retention capability of these areas.

For turbot larvae (Scophthalmus maximus) it has been shown that an increased food concentration very early in life (day 4-7 post hatching) has significantly larger effects on growth of the larvae than an increased food concentration just a little later in development (day 8-11 post hatching) (Steenfeldt, 1991).

The transition zones in the Buchan area are able to hold herring larvae back for several weeks. The larvae seem to concentrate just on the inshore side of the transition zones and a higher standing stock of algae and a higher production of copepod nauplii in one transition zone in a post-storm period have been demonstrated. Still, food was limiting and the larvae were showing sub-optimal growth. (Kiorboe et.al., 1986, 1987, 1988).

**CONCLUSION**

As the very early period in larval life seems to be important for the recruitment, it seems that even if there is a mis-match, concerning large geographical areas, there can in fact still be a perfect match in local areas. Consequently an elevated production of food in a very short period of time during early larval life may determine recruitment success.

The herring seems to spawn in areas where there is potential for a high production of food organisms, and it may be the timing of
the appearance of the herring larvae to these short periods of high production that determines stock size.

**How to create a "match" situation in cultures of *Chicoreus ramosus*?

**Sterile cultures.**

The problems with rearing *Chicoreus ramosus* through out the early critical period may be solved in two different ways. Either through intensive culturing of the larvae as well as their food, or by using an extensive approach, as has been demonstrated with turbot (Paulsen et al., 1989). The intensive culturing system demands microalgae cultured in a sterile or "pseudo-sterile" environment. It is possible to run low-cost, small-scale experimental units for the larval rearing experiments.

Metamorphosed *Chicoreus* are carnivorous contrary to the commercially cultured species in Thailand, and a suitable diet must be supplied to the culturing system at the time where the larvae moves up the trophic chain and become carnivores. Feeding with non-live food in such small scale experimental units will undoubtedly lead to contamination of the water followed by mass mortality. Consequently, a live food organism suitable for the larvae must be found.

"Frontal area" cultures.

The second approach to the rearing experiments would be to simulate the processes taking place in the frontal areas described above. Frontal areas are important larval growth areas in nature and a simulation of the processes of importance in these areas may lead to successful rearing of the larvae.

A meso-cosmos system is a system based on a large water volume with a natural algal composition where the algae are held in the photic zone simply because of low water depth in the tank. This stable "high illumination effect" is comparable to the water held in the photic zone by the stratification of the water column in the frontal area. The nutrient input which increases production in the frontal area, is simulated by renewal of the water with new nutrient rich water.

If much water is exchanged daily, the system will flush and a higher concentration of algae will not be established in the tanks compared to the water pumped from the sea. In order to maintain high production in the system a regeneration of metabolites must be established through an addition of zooplankton to the system. If such a system can be managed a continuous successional pattern of algal species may take place and the larvae will hatch in an environment suitable for survival and growth through the critical phase.

**REFERENCES**


**QUESTIONS AND ANSWERS**

Pitiwong Tantichodok: The match mis-match theory not only concerns the timing of appearance of larvae in a period of high production, but also includes a successional point of view, where the timing of appearance of larvae must take place at a time where there is a production of a suitable food source (algal species). How can you be able to control that it is the right food source that "peaks" in standing stock when your larvae need that particular sized food organism? **Answer:** The management of a poly-culture system is very complex, and it is evident that full control of the composition of different algal species can not be accomplished as it can in a mono-culture system. But a poly-culture system has the advantage of having "a little of everything", resulting in a more complete nutritional composition of the phytoplankton. Larvae have large relative growth rates, and as a result of this they change their retention-spectra continuously through early life. Consequently, they may have an advantage in a poly-culture where new and more suitable algae will be available as the smaller ones are grazed. Of course it is important that the system is not stocked with too high densities of larvae, as this may result in over-grazing of the algae.