# Epipelagic fish production in the open Subarctic Pacific: bottom up or self-regulating control?

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We discuss the processes regulating the production of epipelagic fishes in the northern North Pacific, especially (but not limited to) salmonids, and whether this regulation is likely to be exerted predominately by plankton production processes or self-regulated by the influence of fish on their prey. This question is at the core of the PICES CCCC program, i.e. *Carrying Capacity* and Climate Change.

How is the carrying capacity regulated - by physical and resulting food-web processes ("bottom-up"), or by the effects of variable fish abundance and predation on their prey? If it is from the bottom-up, then one would expect direct linkages with climate variability. If it is regulated by fish abundance (in effect "top-down" control, or perhaps better described as "self-regulating" control), linkages with climate variability may be less direct and anthropogenic effects, e.g. fishing, changes to habitat and rearing conditions, etc., may be more important.

Fig. 1. CZCS satellite images of North Pacific chlorophyll climatology (1978-1986): Winter (top panel), Summer (bottom panel). Chlorophyll colour bar to the right (mg/m³). Images courtesy of Gene Feldman (NASA).
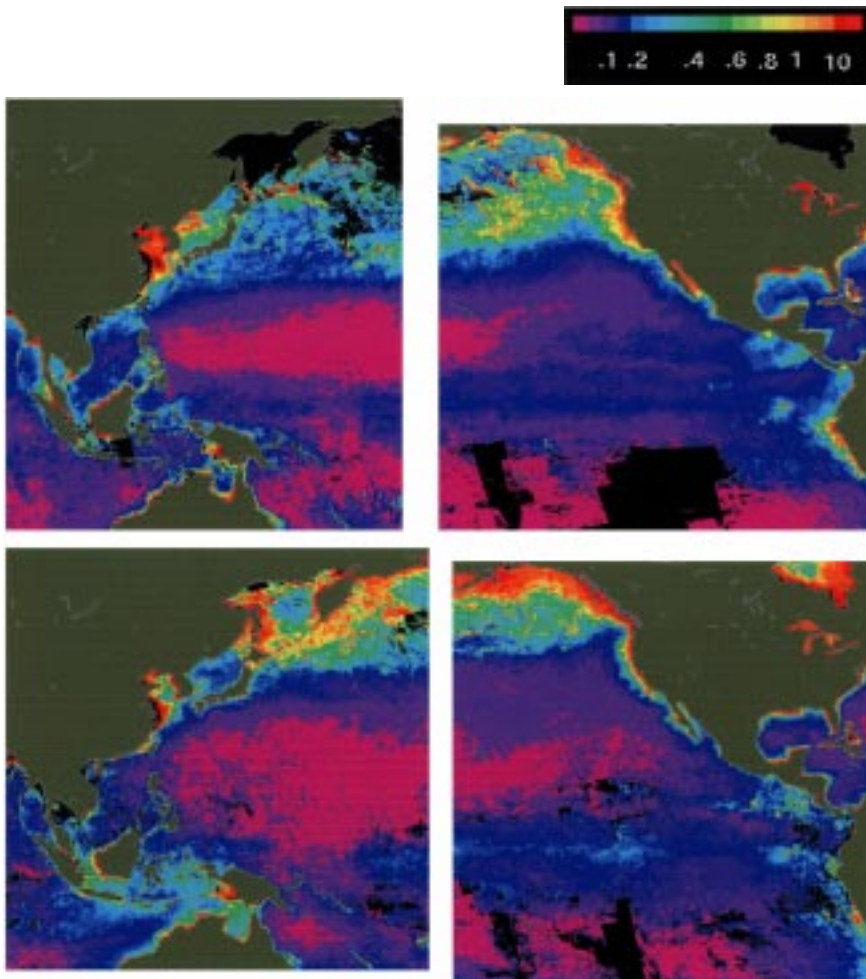
"Bottom-up" Control

Studies of plankton in the North Pacific suggest that production processes may differ between the western and eastern regions, but that the temporal trends have generally been similar from the 1950's at least to the late 1980's. Winter chlorophyll is a particularly good indicator of these regional differences, being low in the western North Pacific and higher in the eastern side, especially in the southern Subarctic and Transition zones (*Fig. 1*). Phytoplankton in the western Subarctic Pacific (in particular the Oyashio Current region) have "traditional" spring bloom dynamics (e.g. Kasai *et al.* 1997) leading to the typical large phytoplankton - macrozooplankton - fish food web. In the early 1980s, phytoplankton biomass in the eastern Subarctic Pacific was considered to be kept low and constant year-round by a shallow mixed layer (in winter) and macrozooplankton grazing in spring, summer and fall (e.g. Parsons and Lalli 1988). The rapid increase in spring grazing pressure by macrozooplankton necessary to prevent a spring phytoplankton bloom was believed to be related in part to large calanoid copepods, whose arrival in surface waters after overwintering at depth was timed to take advantage of the spring increase in primary production.

However, recent studies at Station P in the eastern North Pacific by Project SUPER and the Canadian JGOFS and GLOBEC programs (Booth 1988; Booth *et al.* 1988;

Miller 1993; Boyd *et al.* 1995a,b) have determined that small phytoplankton (<5 (m) are the largest contributor to phytoplankton biomass in the eastern Subarctic region. One regulator of the biomass of this small phytoplankton is microzooplankton, whose grazing rates appear directly coupled to phytoplankton growth rates thereby preventing phytoplankton blooms. The microzooplankton are eaten by macrozooplankton, which are then eaten by fish; however, the abundance of the dominant macrozooplankton (large calanoid copepods such as *Neocalanus* spp.) varies seasonally due to the existence of a deep overwintering phase, which reduces grazing pressure on the microzooplankton during winter. Therefore, the view of phytoplankton biomass variations at Station P (representing the eastern Subarctic Pacific) must be modified to involve small phytoplankton and microzooplankton, as well as macrozooplankton and fish, thereby lengthening the food web and reducing its potential productive capacity for fish. The negative effects of this longer food web may be offset by the recent recognition that primary production in the eastern Subarctic Pacific may have been underestimated by 50% possibly due to the employment of trace metal clean techniques to measure primary productivity (Wong *et al.* 1995).

Concurrent with recognition of the importance of small phytoplankton and microzooplankton has been the recognition of the role of iron in stimulating the production of large phytoplankton such as diatoms in the eastern Subarctic Pacific (e.g. Martin *et al.* 1989; Boyd *et al.* 1996). Large diatoms have higher iron requirements than small phytoplankton (Muggli *et al.* 1996, Muggli and Harrison 1996). Consequently, the growth of large phytoplankton is iron-limited (except for winter), whereas small phytoplankton are not iron-limited and are growing at their maximum rates. However, their biomass is controlled by micro-zooplankton and hence nitrate is not completely consumed as one would expect in the spring and summer. Therefore, increases in large phytoplankton at Station P may be induced by inputs of iron; possible sources for iron include atmospheric transport and deposition (Duce and Tindale 1991), and vertical and horizontal advection. In addition, modeling studies are showing that both sinking of particulate matter out of the photic zone and input of iron into the photic zone are necessary to reproduce the annual phytoplankton and nutrient cycles (*Fig. 2*).

Plankton production in the eastern Subarctic Pacific therefore appears to be controlled by some combination of iron limitation and grazing. Micro zooplankton biomass appears to be regulated by the growth rate of small-celled phytoplankton and the water temperature
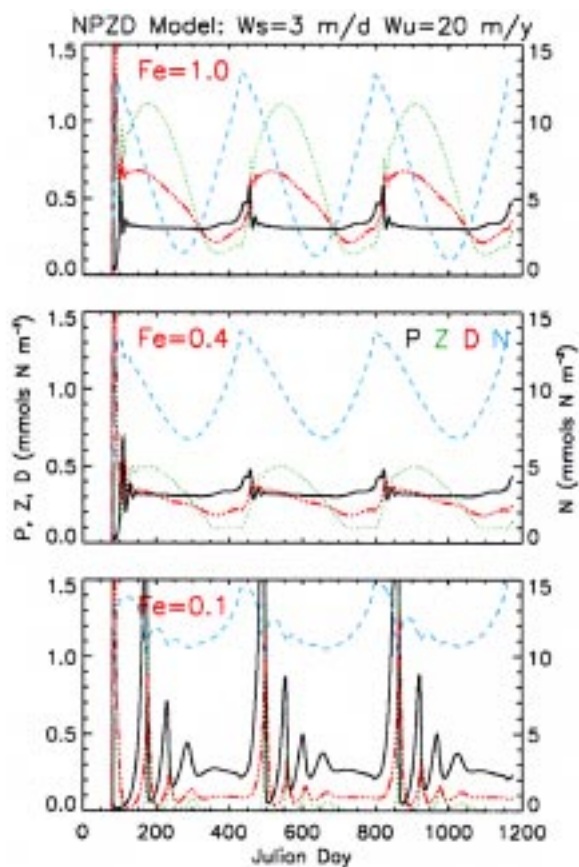

Fig. 2   Upper mixed layer time series (3 years) from a coupled ecosystem (Nitrogen-Phytoplankton-Zooplankton-Detritus) / mixed layer model for the eastern subarctic Pacific. In all three panels the detrital particles are sinking with a speed of 3 m/day and 'remineralizing' (redissolving back to the nutrient pool) with a time scale of 10 days. The nitrogen lost as sinking particles that exit the model (at 120m depth) is replenished by Ekman upwelling of 20 m/year at the bottom of the model. In the top panel there is no iron limitation and the summer mixed layer nitrate (dashed blue line) drops to nearly 1 mmol N m^{-3}, far below the value of about 7 to 8 observed at Station Papa. In the middle panel, low iron limits primary production to 0.4 of its maximum value, even in full sunlight - yielding a realistic annual cycle in nitrate. In the bottom panel, low iron limits primary production to 0.1 of its maximum rate - the summer nitrate concentration is too high, and the phytoplankton biomass (solid black line) undergoes wild oscillations (unlike at Station Papa), probably because iron limits primary production even in winter, causing zooplankton (dotted green line) to drop so low in winter that they cannot graze down the spring bloom of phytoplankton as it develops. (Figure from Denman and Peña 1998)

in winter, and by the increasing biomass of macrozooplankton (their predators) in spring and summer. However, the mixed layer at Station P (and by inference over much of the NE Pacific) has been shallowing with a trend of about 60 m per century, but also with large multi-year variations about this trend (Freeland *et al.* in press). Gradual shallowing of the mixed layer could lead to an increase in diatoms for two reasons: an increase in iron since (assuming a constant supply rate) it will be dissolving in a smaller volume, and an increase in the amount of time that phytoplankton spend above the compensation depth. Increases in diatoms would shift the food web towards the large phytoplankton-macrozooplankton-fish linkages and, since it is a shorter link, to higher production of epipelagic fishes. It also suggests that production processes in the western and eastern North Pacific may converge towards similar plankton dynamics.

Shallowing of the mixed layer at Station P may also lead to warming of the upper layer as the solar heating becomes distributed over a smaller volume. Warmer temperatures have been associated with earlier average timing of development in copepod populations in the Subarctic North Pacific, with the result that the date of peak biomass has moved almost two months earlier since the 1970's (*Fig. 3*). If warmer temperatures in winter also increase microzooplankton growth and abundance, then the earlier spring peak in copepod biomass might also translate into better copepod survival. A relationship between increased zooplankton biomass and increased sea temperatures on the temporal scale of the quasi-biennial oscillation (average 28 months) has recently been identified by Conversi and Hameed (1997) using data from Station P for the period 1957-1980.

These processes suggest a trend towards increased macrozooplankton abundance, and therefore towards an increased potential for production of fish in at least the eastern Subarctic Pacific. Studies by Brodeur and Ware (1992, 1995) and Sugimoto and Tadokoro (1997) suggest that zooplankton and epipelagic fish production has indeed increased throughout most of the northern North Pacific between the 1950's and the 1980's. Wong *et al.*(1995) noted that estimates of primary production in the eastern Subarctic Pacific in the period 1984-90 were double the estimates made during 1960-76. However, it was unclear whether such a change was due to climatological effects, such as increased atmospheric circulation and increased inputs of wind-borne iron, or whether it was due

mostly to improved methodologies for estimating production. The higher zooplankton biomass through the 1980's has been suggested by a number of studies (e.g. Beamish and Bouillon 1993; Hare and Francis 1995) to have supported the higher abundance of salmonids that have occurred throughout the North Pacific during the 1980's. The question then arises as to whether such high abundance of epipelagic fishes are likely to limit the abundance of their prey, and in turn their own abundance.
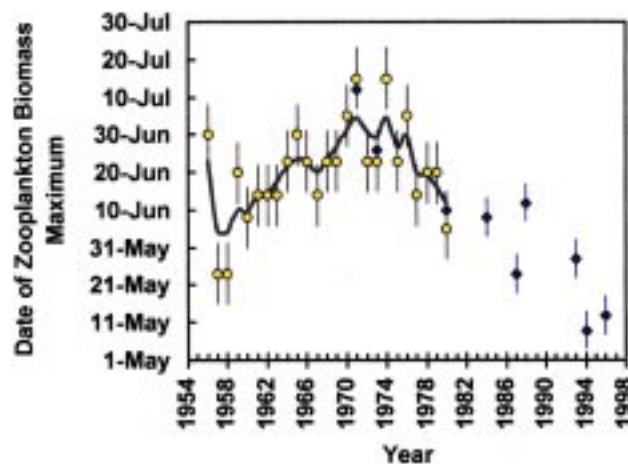

Fig. 3 Interdecadal change in timing of the spring-summer zooplankton maximum at Ocean Station P. Seasonal development of the zooplankton population was very late in the early 1970s, but by the mid 1990s had shifted about 60 days earlier. Circles show annual timing based on biomass measurements from the 1956-1980 Canadian weathership time series. Diamonds show timing estimates based on copepodite stage composition (from Mackas, Goldblatt and Lewis, in review). Line is smoothed fit to the weathership time series estimates.

Self-Regulating" Control

A variety of species dominate the epipelagic fish fauna of the Subarctic and Transition zones in the Northern Pacific (Brodeur 1988; *Table 1*). Salmonids are an important component of this fauna, making up 90% or more of surface net catches in the Subarctic Pacific. Unfortunately, modern sampling gear still does not allow an accurate comparison of the biomass of vertically migrating myctophids, or the biomass of the much faster moving squids, so the relative impact of these species groups on controlling macro-zooplankton abundance is difficult to assess. There is some evidence that large abundance of epipelagic fishes can influence the biomass of their macro-zooplankton prey in the North Pacific. Cooney (1988) identified a weak but significant correlation between Station P zooplankton biomass (1955 to

Table 1. Dominant epipelagic fishes in the Subarctic and Transition zones of the North Pacific Ocean. Modified from Brodeur (1988).

Scientific Name	Common Name	Subarctic or Transitional
Lamna ditropis	salmon shark	both
Prionace glauca	blue shark	both
Oncorhynchus keta	chum salmon	Subarctic
O. gorbuscha	pink salmon	Subarctic
O. nerka	sockeye salmon	Subarctic
O. kisutch	coho salmon	Subarctic
O. tshawytscha	chinook salmon	Subarctic
Salmo gairdneri	steelhead trout	Subarctic
Cololabris saira	Pacific saury	both
Trachurus symmetricus	jack mackerel	Transition
Scomber japonicus	Pacific mackerel	Transition
Brama japonica	Pacific pomfret	both
Thunnus alalunga	albacore tuna	Transition

1980) and North American pink salmon abundance, with lower zooplankton abundance occurring one year after high pink salmon abundance. He did not find, however, a significant relationship between Station P zooplankton abundance and the growth of pink salmon. Shiomoto *et al.* (1997) described an alternating cycle of high zooplankton biomass in the western North Pacific concurrent with low phytoplankton biomass in one year, followed by low zooplankton biomass and high phytoplankton biomass the next year, which they suggested was driven by predation of pink salmon on zooplankton, forced by the 2-year variation in strong and weak Asian pink salmon abundance. Odate (1994) also observed inverse spatial variations in the abundance of large phytoplankton and macro-zooplankton in the central North Pacific, and speculated that feeding by Pacific saury on macrozooplankton reduced zooplankton biomass resulting in higher abundance of large phytoplankton.

All of these studies address the potential effect of high epipelagic fish abundance on their macrozooplankton prey (a true "top-down" effect), so that phytoplankton abundance appears to vary in phase with the fish. But do these variations in plankton biomass affect the growth and survival of fish? There are some indications that the amount of food in the stomachs of chum, pink, and sockeye salmon varies inversely with the abundance of pink salmon, particularly in the western North Pacific (Sano 1963, Heard 1991, and Burgner 1991, respectively). Retrospective studies also suggest that the terminal size of some species of salmon is lower in years when the abundance of pink salmon is high (e.g. Ogura 1991, Bugaev *et al.* (submitted)).

Ito (1964) suggested this type of variation was due to changes in diet, from squids in years of low pink salmon abundance, to zooplankton in years with high pink abundance. Perhaps the best example of the "self-regulating" effect of high pink salmon abundance on other salmon is the study of Tadokoro *et al.* (1996), which observed clear changes in the diet of chum salmon in the central Subarctic Pacific from predominately gelatinous zooplankton when Asian pink salmon were abundant to predominately crustacean zooplankton when pinks were not abundant. They argued this switch was forced by severe depletion of crustacean zooplankton by the abundant pink salmon. It is noteworthy that most of these observations relate to the effect of Asian pink salmon, which may be a result of their very large relative abundance in alternate years, which makes an effect easier to detect.

The observations of salmon grazing affecting zooplankton abundance, and potentially influencing salmon feeding, is rather surprising at first inspection. Calculation of zooplankton abundance in the North Pacific suggests that there is much more plankton available than can possibly be used by the salmon biomass (Sanger 1972). If salmon are broad spectrum and relatively unselective feeders, why should they show growth responses to their own abundances? In the North Pacific, maturing salmon appear to be opportunistic feeders, with the major prey items being (first) squid and fish, followed by euphausiids and amphipods, and only later by copepods (e.g. Pearcy *et al.* 1988; Heard 1991). However, at younger ages the diet may contain primarily macrozooplankton, and different species of salmon show evidence of trophic partitioning, suggesting that significant competition may occur in at least some areas and times. The latter observations are especially true for chum salmon, which do appear to specialize in feeding on gelatinous zooplankton and associated crustaceans (e.g. Welch and Parsons 1994). If the abundance of plankton is not affected by salmon abundance, there seems little reason that evolutionary pressure would have selected for some of the marked anatomical specialization seen in chum that help in feeding on gelatinous zooplankton (e.g. Welch 1997).

Concluding Comments

At some point, the ability of the open Subarctic Pacific to produce epipelagic fishes must be limited.

The question we have considered is whether this limitation is most likely to be due to constraints on the basic production of food (from phytoplankton to fish) or to the possibility that high abundance of fish "self-regulate" their production by over-grazing their prey. Observations of strong and concurrent increases in zooplankton and fish biomass on decadal scales (e.g. Brodeur and Ware 1992, 1995) argue for the direct food web effect (bottom-up control), but the picture is complicated by the differences in food web dynamics between the western and eastern Subarctic Pacific.

There is some evidence for top-down control of zooplankton biomass, mostly in the western North Pacific in relation to very large abundance of Asian pink salmon. The principal effect of this on salmon themselves appears to be a shift in the major dietary items, which in turn can cause lower weights of stomach contents. However, it is not clear that this is reflected in lower survival rates. The opportunistic nature of salmon feeding may serve to buffer them from major fluctuations in the availability of particular prey, but here again large interannual variation in size suggests that growth must be coupled with food abundance. The high importance of squid in the diets of all salmon (except chum) suggests more attention should be paid to this trophic level in the high seas; this attention appears to be lacking within the PICES CCCC program at present.

Distinguishing bottom-up or self-regulating control of epipelagic fish production in the open North Pacific is not simple. One difficulty is determining what fraction of secondary production is consumed by other species, in particular the vertically migrating mid-water fishes such as myctophids. Seasonal migrants that move between the Transition and Subarctic zones will also cause a net loss of secondary production from the Subarctic region. Another difficulty is identifying when control on fish production has been exerted by food web processes, or by the fish themselves. For example, if fish production were limited by bottom-up processes, the responses in fish should be independent of fish density, although these responses may be more severe when fish density is higher.

If fish production were limited by fish density (e.g. by reducing prey abundance), then the effect should be most apparent at very high fish densities. Therefore, observations of *consistently* declining size-at-age or ocean survival may be indicative of bottom-up limitation. We are not suggesting that density-dependent effects of salmon (i.e. influences on salmon

growth and survival that occur as a function of fish density or abundance) do not occur, but that it may be a question of where and when during the life history such effects may be most important. For example, on-going work within the Canadian GLOBEC program (*Fig. 4*) suggests that growth of salmon (at least for some species and stocks) may be regulated more during their out-going and in-coming migrations along the continental shelf than by their time in the open Subarctic Pacific.
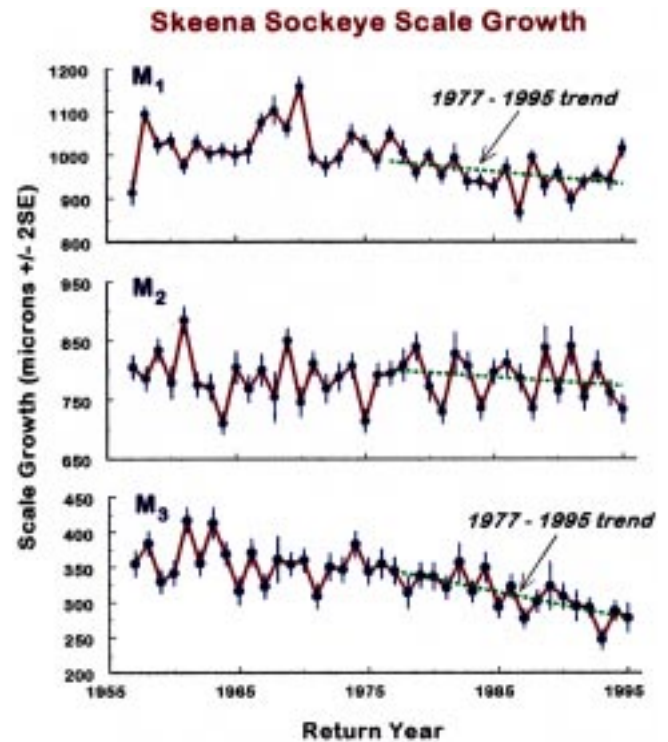

Fig. 4   Changes in salmon growth, measured as width of the annual rings on scales for Skeena River. (B.C.) salmon. Note that a long-term trend towards lower growth rate is evident for the first (M_1) and last (M_3) years of life in the ocean, but not the second (M_2) year. This suggests that growth conditions in the coastal environment may be uncoupled from those in the offshore, and that the "carrying capacity" concept may need to incorporate the possibility of different carrying capacities in different regions of the Pacific, rather than a single homogenous whole.

Summary

We conclude that the production of epipelagic fishes in the Eastern Subarctic Pacific, especially (but not limited to) salmonids, is likely to be controlled by bottom-up (food web) processes rather than self-regulated by the effects of fish abundance on their zooplankton prey (e.g. "self-regulating" control), at

least when considered over the entire life history and entire North Pacific Ocean. While there are indications that exceptionally high abundances of salmon can affect the abundance of (local) zooplankton resources, this seems unlikely to be a dominant influence controlling the structure and functioning of epipelagic fish production in the Subarctic Pacific ecosystem. We agree with the comment by Sugimoto and Tadokoro (1997) that bottom-up control may be most influential on decadal and longer time scales. Although these authors also suggest that top-down predator control may be the dominant source of short (biennial) fluctuations in zooplankton and phytoplankton biomass in the Northern North Pacific, we believe that broad scale plankton dynamics, such as those associated with inputs of iron and microzooplankton grazing in the eastern Subarctic Pacific, are likely to dominate generally. However, an important issue that still remains to be resolved is the possibility of area-specific "bottlenecks" to production, such as shelf vs open-ocean, particularly when considered in the context of possible differences in spatial distribution and trophic overlap.

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