Physics to Fish: Interactions Between Physics and Biology on a Variety of Scales

By Ann E. Gargett

PHYSICAL PROCESSES are of major importance to marine ecosystems because marine plants have neither root nor branch. Unlike their terrestrial counterparts, they cannot use stems or branches to position themselves favorably in the sunlight, nor roots to tap the wealth of nutrients that lie below the ocean nutricline. Instead it is physical processes that provide the nutrient and light environments that shape marine ecosystems from their base in primary production.

The important physical processes act at all scales. At the largest spatial scales (Fig. 1), wind-driven upwelling positions the nutricline quite close to the euphotic zone in subpolar gyres. Although such gyres are consequently rich in nutrients, primary production can be light-limited at least part of the year at these high latitudes. In contrast, light levels are higher and more constant throughout the year in subtropical gyres, but the nutrient supply is meager, because downwelling places the nutricline well below the euphotic zone.

Whether the nutricline is shallow or deep, the actual vertical transport of nutrients up into the euphotic zone occurs through the action of small-scale physical processes, generally lumped together under the word "turbulence." Over the past two decades, physical oceanographers have become increasingly able to measure such processes in the upper ocean, using various fields measured from freefall microscale profilers, supplemented more recently by a variety of innovative new techniques involving acoustics (Gargett, 1997a and the article by Farmer in this issue—*Observing the Ocean Side of the Air-Sea Interface*). Depending on the relative location of the base of the surface mixing layer and the top of the nutricline, nutrients are resupplied to the euphotic zone by a variety of small-scale processes—near-surface turbulence driven by winds or breaking waves, Langmuir cells, shear instabilities at the mixing layer base, free convection driven by surface heat loss or salinization, and, where mean gradients are suitable, the double diffusive processes described in *Differential Fluxes of Heat and Salt: Implications for Circulation and Ecosystem Modeling* by Barry Ruddick, this issue.

Turbulent processes also modulate the light environment of phytoplankton by moving them in the strong vertical gradient of near-surface light. The importance of light to primary productivity is shown by classic P versus I curves (Parsons *et al.*, 1977) in which productivity P increases strongly as light intensity I increases, to a maximum that depends on the individual species. Even with a single species, however, photosynthetic response in the real ocean is a more complicated tale, because P depends not only on intensity but also on how long a given intensity level is maintained. The classic result is obtained when lab cultures are grown at intensity I for a *short period* of time, on the order of 10 min. However, when measured over *longer exposures*, on the order of hours, these cultures exhibit photo-inhibition, where productivity falls with increased light, and falls further the higher the light level (Marra, 1978).

Time scales on the order of 10 min are reasonable for variations associated with the largest turbulent eddies that advect phytoplankton in the near-surface mixing layer. However, the longer time scales, on the order of hours, are also relevant to light variation in the real ocean. Figure 4

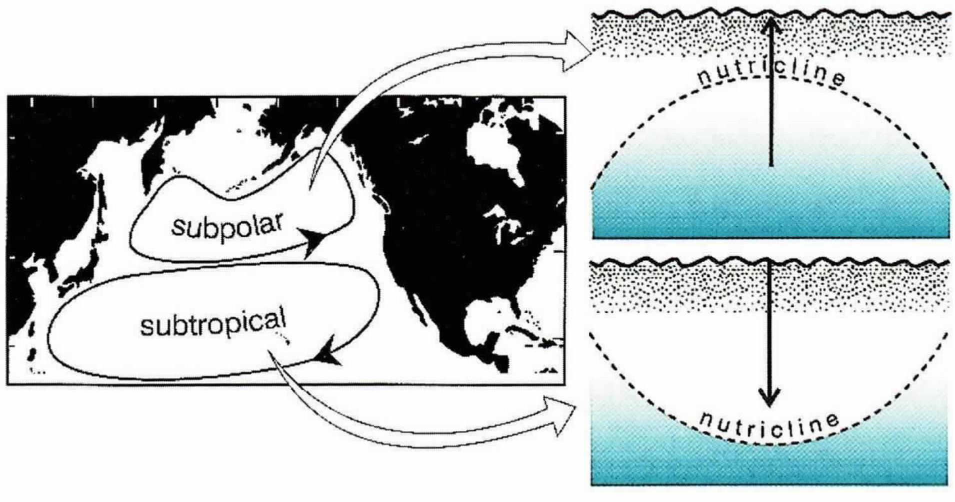

Fig. 1: Wind-driven upwelling and downwelling in the major ocean gyres sculpt the surface of the nutricline, moving it respectively closer to and farther from the sea surface within subpolar and subtropical gyres. As a result of these large-scale characteristics of the physical system, the euphotic zone in subpolar gyres is macro-nutrient replete, whereas that in the subtropical gyres is relatively nutrient-starved.

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of Wilf Gardner's article *The Flux of Particles to the Deep Sea: Methods, Measurements, and Mechanisms* (this issue) shows the spaghetti-like tracks made by depth histories of many individual neutrally buoyant floats, ballasted to move with the water and tracked acoustically over several days of low wind speed (D'Asaro *et al.*, 1996). Any single composite, such as the one highlighted in this figure, may be thought of as a possible depth history of a single phytoplankton cell throughout a typical day. At night, heat loss from the surface drives convective motions that move cells progressively farther from the surface, to depths on the order of 100 m. Soon after sunrise, heating at the surface damps out the convective motions, and cells near the surface remain trapped there by formation of a shallow diurnal thermocline, until convection resumes shortly after sunset. One can immediately appreciate the relevance of time scales on the order of several hours in the context of such diurnal variability in near-surface stratification.

Such particle tracking measurements also illustrate a very general result, namely that the small-scale physical processes that shape the nutrient and light environment of the upper ocean are strong functions of near-surface stratification. Strong vertical stratification severely inhibits the vertical motions associated with turbulence, and thus the associated vertical turbulent fluxes. In contrast, where water columns are weakly stratified, vertical excursions and fluxes may be large. As illustrated in Figure 2, this general result can be used to form a very simple conceptual summary of the interaction between physics, represented by water column stability, and biology, represented by primary production. When upper ocean stability is extremely weak, production is low because, although large vertical fluxes provide plenty of nutrients, large vertical excursions result in low average light. Production is also low in conditions of very high stability, where small vertical velocities lead to adequate light but fail to supply sufficient nutrients. *Both* light and nutrients will be adequate at intermediate stabilities, within an "optimal stability window" (Gargett, 1997b).

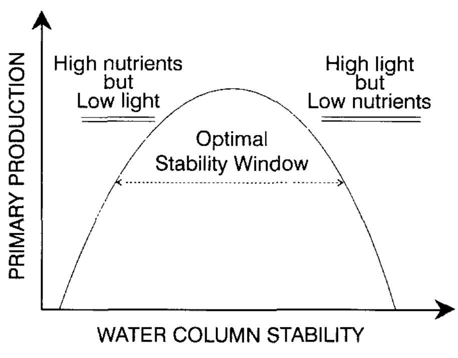

Fig. 2: Schematic of an optimal "window" in water column stability, a physical environmental variable that has both positive and negative effects on primary production. By restricting vertical motions and fluxes associated with turbulent processes, increased stability brings an increase in the average light seen by a phytoplankter (positive), but a decrease in the resupply of needed nutrients (negative). Any such variable is associated with a "window" at intermediate values, within which production is maximal.

Although the preceding discussion gives the impression that marine biology consists only of phytoplankton, anyone who reads newspapers even occasionally can't fail to notice that ordinary people are interested in marine ecosystems at a level much higher than that of phytoplankton—they're interested mostly in fisheries. Once one moves this far up the food chain, there are many factors that contribute to the size of marine fish stocks over time—predation, commercial, and recreational fisheries, and habitat destruction, to name but a few. However, over the past several years, evidence has been accumulating to suggest that climate variability on decadal time scales is an additional and strong influence on the size of marine fish stocks (Beamish, 1995).

The example I will use here, illustrated in Figure 3, is the apparent variation in total production of North Pacific salmon stocks (represented as the mean annual catch of the major fishing nations), with an index related to the strength of the wintertime Aleutian Low pressure system that dominates atmospheric circulation in the North Pacific in the winter and spring (here the index of Beamish and Bouillon, 1993). The correlation between these two time series is such that the total catch is high during periods of intensified winter low pressure in the Gulf of Alaska (large values of the Aleutian Low Pressure Index, ALPI). Although one must certainly be wary of a correlation over what amounts to little more than one cycle, this is only one of several pieces of evidence that point to some connection between the success of salmon stocks in the North Pacific and the state of the overlying winter/spring atmosphere.

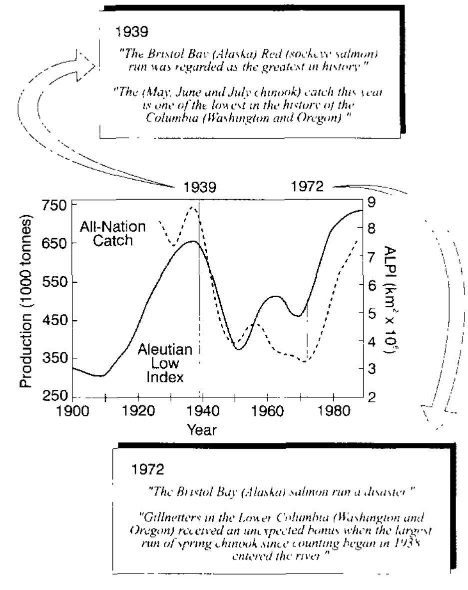

Fig. 3: Time series of the production of North Pacific salmon, estimated as the annual all-species catch of the major fishing nations (dashed line), and the Aleutian Low Pressure Index (ALPI: solid line) of Beamish and Bouillon (1993) appear to be roughly correlated, suggesting some connection between the strength of winter/spring atmospheric forcing of the North Pacific Ocean and the success of North Pacific salmon stocks. Anecdotal information (abstracts from the "Pacific Fisherman" by Mantua et al.*, 1997) suggests that this connection operates to produce out-of-phase fluctuations in northern and southern stocks.*

This connection, whatever it may be, appears to change phase between the northern and southernmost range of salmon habitat in the North Pacific, an added complexity that is obscured in the values for total catch, but appears in the anecdotal information shown in Figure 3. Other more quantitative evidence (Francis and Sibley, 1991) suggests the same thing, namely that when the northernmost (Alaskan) Pacific stocks do well—e.g., in 1939, a time of generally *strong* Aleutian Lows—southern stocks (in Washington, Oregon, and northern California) do poorly, and *vice versa*.

To proceed beyond such correlations, we need answers to three questions.

1. WHAT is the actual mechanism involved? Clearly there is a very large mechanistic gap between the state of the

atmosphere and the well-being of a particular fish stock.

2. WHY do northern and southern stocks vary out of phase?

3. WHERE does this mechanism operate?

The last question is a very important one to answer at an early stage, because of the highly migratory nature of salmon stocks. If it is possible to narrow down the spatial location of the major environmental effect on survival, this helps to narrow the search for possible mechanisms. To understand the importance of WHERE, consider the time/space trajectory of juvenile salmon emerging from British Columbia's Fraser River in May. Over the subsequent summer and fall months, their migratory path to the deep ocean is known to be very strongly restricted to the coastal rim of the northeast Pacific, at least as far as Kodiak Island. Many different pieces of evidence suggest that survival rates are determined mostly during the first year of ocean life (Francis and Hare, 1994; Gargett, 1997b), so that this trajectory and its timing imply that the mechanisms affecting survival most likely operate in the *coastal* ocean.

With this answer to WHERE, a possible answer to WHAT and WHY comes from returning to the level of primary production and the idea of competing effects of water column stability on nutrient and light supplies, as summarized in the "optimal stability window" of Figure 2.

Given the mean nutrient and light supplies that are known to be characteristic of subpolar and subtropical gyres, it seems reasonable to assume that phytoplankton populations in these **N** (Northern, subpolar) and **S** (Southern, subtropical) gyres exist toward opposite ends of this window (Fig. 4a)—with the subpolar coastal populations limited mainly by light, the subtropical ones by nutrients.

Imagine now what happens if water column stability *increases* everywhere in the N. Pacific (Fig. 4b). As the environment of the **N** populations becomes more stratified, they move into more favorable conditions (as higher stratification brings higher light levels), whereas **S** populations move to less favorable conditions (as higher stratification lowers the nutrient supply). The opposite happens if stability decreases everywhere (Fig. 4c)—**S** phytoplankton populations thrive and **N** populations struggle. This can be directly translated to a mechanism for out-of-phase variation in **N** and **S** fish stocks, linked to the strength of the wintertime Aleutian Low, *if*, as assumed in the secondary labeling of Figure 4:

1. it is possible to make a linear connection up a simple food chain (so that more phytoplankton means more zooplankton, means more fish survive), and
2. it can be demonstrated that the strength of the winter/spring Aleutian Low is directly related to *coastal* ocean stability over the full N/S extent of the eastern border of the North Pacific.

Since a simple food chain is reasonable for salmonids, let's just consider the second point, i.e., a possible basis for a relationship between coastal stability and the Aleutian Low.

Figure 5 illustrates the dominant characteristics of the wintertime atmosphere in the northeast Pacific during periods of strong and weak Aleutian Low (taken from the series of winter-average surface pressure maps for 1947–1982 given by Emery and Hamilton, 1985), and consequent effects on coastal ocean stability. A strong Low brings intensified flows of moist marine air up against the coastal mountains of Alaska and northern British Columbia (B.C.). In these northern regions where ocean density is mostly determined by salinity, the coastal ocean should become more strongly stratified under these conditions, due to increased precipitation and run-off. A strong Low also displaces the California high pressure system to the southeast, bringing increased incidence of southerly winds to the coast of California. In regions on the eastern edge of the subtropical gyre, coastal stability is most strongly influenced by upwelling; an increased incidence of southerly winds means less upwelling, hence here too a more strongly stratified water column. Conversely, during periods when the Aleutian Low is weak, winter winds across the North Pacific are much more zonal, the main flow of marine air impinges on the coastal mountains in southern B.C., Washington, and Oregon, while Alaska experiences generally dry continental outflow winds. The California High moves back offshore and northerly winds return to the California coast. Decreased freshwater input in the north and increased upwelling in the south bring weaker stratification along the entire eastern coastal boundary of the North Pacific.

Do observations support this hypothesized in-phase variation of coastal stability as a function of the strength of the winter/spring Aleutian Low? A time series of what we want, i.e., water column stability, is not available over the re-

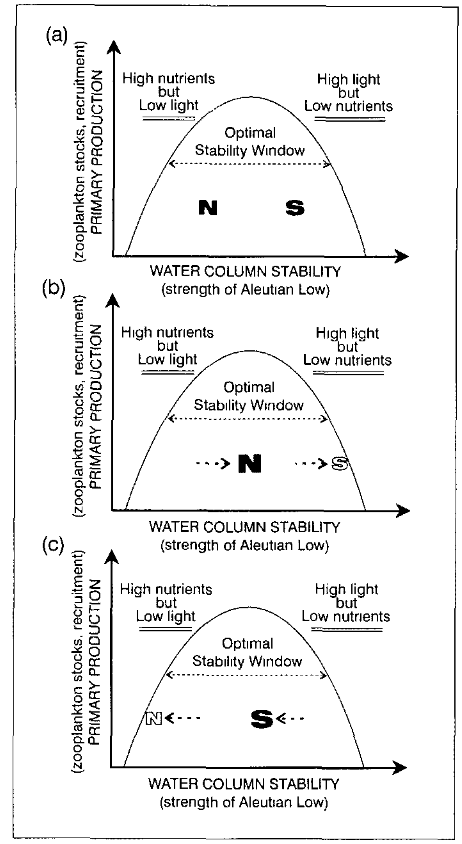

*Fig. 4: (**a**) Considering the general characteristics of subpolar and subtropical gyres, it seems likely that canonical northern (**N:** Alaska, subpolar gyre) and southern (**S:** northern California, subtropical gyre) phytoplankton stocks occupy respectively the low-stability and high-stability ends of an optimal stability "window." (**b**) If water column stability increases everywhere, northern stocks will move toward optimal conditions, while southern stocks move out of the "window" toward less favorable conditions. (**c**) The opposite happens when water column stability decreases: southern stocks will flourish while northern ones struggle. It is believed that the major oceanic effect on salmon survival rates occurs during the first year of ocean life, spent mostly in coastal waters: the "window" concept implies that if water column stability varies in-phase over the entire eastern coastal North Pacific, **N** and **S** coastal primary production (hence, it is assumed, secondary production and salmon survival) will vary out of phase.*

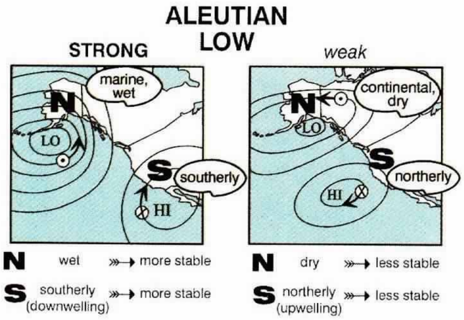

Fig. 5: Idealizations of the states of the atmosphere/ocean system during relatively strong and weak states of the winter-spring Aleutian Low and associated California High. An intensified (strong) Aleutian Low brings above average stability to the subpolar coastal ocean through above-average precipitation and run-off. The associated south-eastern displacement of the California Low brings more southerly (downwelling-favorable) winds to southern coastal regions; any decrease in upwelling results in more stable coastal water columns in the subtropical gyre. In the weak state, outflow winds bring dry continental air to Alaska; decreased precipitation lowers coastal ocean stability throughout the eastern subarctic gyre. Offshore movement of the California High returns northerly (upwelling-favorable winds) to southern regions, moving deeper, more weakly stable water toward the surface. Such variation in the state of the atmosphere could thus produce in-phase variation in coastal water column stability over the entire eastern North Pacific, hence, through the mechanism of the optimal stability "window," the observed out-of-phase variation of northern and southern salmon stocks.

quired decades; instead we are forced to look for available time series that might be expected to act as surrogates. Assuming that high streamflow should produce more strongly stratified coastal waters in the **N** (Gulf of Alaska) and that high temperatures should indicate more strongly stratified water columns in the **S** (subtropical gyre off southern California), such surrogates for coastal water column stability *do* suggest in-phase variation of stability from California to Alaska, and furthermore that stability *is* higher during periods of strong wintertime Aleutian Lows (Gargett, 1997b).

Thus it appears that we have potential answers to the WHAT and WHY questions considered earlier. Atmospheric control of coastal water column stability, hence primary production, is a possible mechanism connecting salmon stocks and the strength of the Aleutian Low. Because this atmospheric forcing acts to produce in-phase variation in stability all along the eastern boundary, **N** and **S** stocks may vary out of phase because of the existence of an "optimal stability window."

The above discussion is focused on a single marine fish stock. It is important to appreciate that the particular mechanistic connection suggested here for Pacific salmonids may be inappropriate for other stocks—those with very different life histories and/or behaviors, or those that are part of complex food webs rather than the simple food chain considered here. In addition to an appreciation of the physical processes that shape the upper ocean biological environment, formulation of possible mechanistic connections between physics and fish requires a significant amount of information about the particular fish species under consideration—even for the commercially important and relatively well-studied Pacific salmonids, it is only recently that there have been enough "fish facts" to constrain potential mechanisms significantly. Finally, it should be emphasized that the particular mechanism suggested here to link atmospheric physics with salmon stocks may itself prove to be right or, more likely, prove to be wrong. Right or wrong, however, any mechanistic suggestion consistent with observations has a very real advantage over correlation methods of investigating connections between physics and fish—namely mechanisms can be tested, by retrospective analyses of existing time series, by testing predictions against future time series, and/or by focused process studies. It is only by such attempts to test specific mechanisms that we will learn more of what we need to know about the complex interactions that underlie apparent correlations between the physical environment and marine fish populations.

References

Beamish, R.J., ed., 1995: *Climate Change and Northern Fish Populations.* Can. Spec. Publ. Fish. Aquat. Sci., *121,* 737 pp.

——— and D.R. Bouillon, 1993: Pacific salmon production trends in relation to climate. *Can. J. Fish. Aquat. Sci., 50,* 1002–1016.

D'Asaro, E.A., D.M. Farmer, J.T. Osse and G.T. Dairiki, 1996: A Lagrangian float. *J. Atmosph. Oceanic Tech., 13,* 1230–1246.

Emery, W.J. and K. Hamilton, 1985: Atmospheric forcing of interannual variability in the Northeast Pacific Ocean: Connections with El Niño. *J. Geophys. Res., 90,* 857–868.

Farmer, D., 1997: Observing the ocean side of the air-sea interface. *Oceanography, 10,* 106–110.

Francis, R.C. and S.R. Hare, 1994: Decadal-scale regime shifts in the large marine ecosystems of the North-east Pacific: a case for historical science. *Fish. Oceanogr., 3,* 279–291.

——— and T.H. Sibley, 1991: Climate change and fisheries: what are the real issues? *N.W. Environ. J., 7,* 295–307.

Gardner, W., 1997: The flux of particles to the deep sea: methods, measurements, and mechanisms. *Oceanography, 10,* 116–121.

Gargett, A.E., 1997a: "Theories" and techniques for observing turbulence in the ocean euphotic zone. In: *Lecture Notes on Plankton and Turbulence,* C. Marrasé, E. Saiz and J.M. Redondo, eds. Scientia Marina, Intl. Centre for Coastal Resources, Barcelona, Spain. *61*(Suppl), 25–45.

———, 1997b: The optimal stability "window": a mechanism underlying decadal fluctuations in North Pacific salmon stocks? *Fish. Oceanogr., 6,* 109–117.

Mantua, N.J., S.R. Hare, Y. Zhang, J.M. Wallace and R.C. Francis, 1997: A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Amer. Meteor. Soc., 78,* 1069–1079.

Marra, J., 1978: Phytoplankton photosynthetic response to vertical movement in a mixed layer. *Mar. Biol., 46,* 203–208.

Parsons, T.R., M. Takahashi and B. Hargrave, 1977: *Biological Oceanographic Processes, 2nd edition.* Pergamon Press, Oxford, 332 pp.

Ruddick, B., 1997: Differential fluxes of heat and salt: implications for circulation and ecosystem modeling. *Oceanography, 10,* 122–127. ❑