Persistence of Fish Populations in Time and Space as a Key to Sustainable Fisheries

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Abstract

The goal of the presentation is to consider future fisheries models that attempt the predictive forward modeling of fish populations in the context of the ecosystem and the fisheries directed towards them. The base models include explicit treatment of spatial distributions in realistic physical settings that are capable of treating climate variations. The populations themselves can be structured in terms of age, metabolism, and genetics. Finally, the models are formulated in a manner that allows a treatment of the direct effects of fishing including factors that control it (i.e. socioeconomic factors). The development of these models includes both examples of simple elementary food webs under the influence of ecosystem forcing (physical and biological) and fishing. The conditions under which these systems are sustainable are discussed. The latter makes use of considerations of the persistence of populations in space and time. Aspects of population dynamics under the influence of different forms of movement in heterogeneous environments and different ways of treating mortality are discussed. An attempt is made to analyze fisheries from the prospective of invasibility of the systems by a fishery and its impact on persistence of simple systems.

Introduction

There has been a growing debate over the status of global fisheries and the degree to which the paradigms of fisheries management developed over the past century have essentially failed. The debate boils down to whether the science, information, and methods used to assess fish stocks and recommend management decisions were inadequate or if the current status of many fish stocks represents a failure in social-political systems and their perchanct to ignore scientific advice (Heinz Center, 2002). Independent of how different stakeholders feel about where the problems lie, there is a growing consensus that there is a need for new approaches to our understanding of fisheries. This has lead to legislative demands such as those in the 1996 reenactment of the Magnussan-Stevens Fisheries Act that fisheries be managed on an ecosystem basis (NCR 1994). In the period since the Act was passed, it has been interesting to watch the various efforts to understand what this means and what new tools need to be put in place to realize true ecosystem based fisheries management.

The presentation here is aimed at considering future progress towards the goal of management of resources and the industries, both extractive and not, that utilize them. The goal is to introduce new modeling approaches that are appearing in the theoretical ecological literature and potentially have promise in fisheries. These encompass methods for expanding on the current state of the art fisheries models such as ECOPATH and ECOSIM (Pauly et al, 1998). It is important to contrast the ECO-class of models with their large number of fishery components with age structure versus the traditional single species models used in fisheries assessment. The ECO models can be viewed as a move to include the multi-species interactions within those species that are involved in

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the relevant systems. In this way ECO-class models expand traditional methods to include connections to entire "fisheries" ecosystems. The design of the ECO models is compatible with existing fisheries statistics. The implementation is, however, not consistent with what one would accept as an ecosystem model with a rather complete treatment of various species and their distribution in space. In fact ECOPATH is a fitting program designed to produce a deterministic appraisal of current fisheries data sets at an ecosystem level. Expanding this in ECOSIM to attempt a prognostic estimate of the future of these systems is a very laudable goal, but one that is unlikely to succeed without further basic developments. Here some of the basic considerations needed for improving ecosystem based models for fisheries are outlined.

With a goal of improving predictive or forward models for fisheries systems in the context of ecosystem dynamics a set of intermediate models is considered here. The models are focused on an explicit treatment of the spatial structure of marine ecosystems with realistic treatment of marine physical settings. The populations themselves are structured (Metz and Diekmann, 1980) in terms of population age structure, metabolism (bioenergetics), and where applicable genetics. An adequate treatment of the forces that distribute populations in space is also crucial (Olson and Hood, 1994). Finally, the direct consideration of the act of fishing is important. The latter is introduced below, but a full socio-economic model is left for further work.

The presentation will begin with a generic model of the simplest fragment of a food web that can be formulated. This includes a three species interaction at at least two trophic levels (Fig. 1) and the action of a fishery. The idea is to analyze this as a component of the large multi-species interactions that show up in the ECO-type models. An example of a structured model that includes explicit population dependence on environmental climate is then given. This is followed by a discussion of issues involved with the dispersal of fish populations due to physical advection and

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migration. The importance of behavioral responses to the biotic and physical environment is then considered. This includes the importance of schooling in determining both the inter-population dynamics in an ecosystem and the degree to which aggregation yields economically viable fisheries. These considerations are followed by a discussion of methods for approaching the problem mathematically. This is followed by several examples of possible applications of intermediate models to existing fisheries problems.

Structured Models

An accurate depiction of the system suggested in Fig. 1 in terms of issues such as recruitment to a fishery, realistic depiction of mortality, and species interaction demands that a model include age (a), a metabolic variable such as weight (w), consideration of the movement of organisms through space, and a treatment of the trophic interactions depicted.

If the ith population level is N_i, the population equation can be written as a partial differential equation involving the other populations (N_j) and environmental variables

$$\dot{N}_i(a,t,x) = f(N_i(a > a_m)) - \mu_i(w_i, N_j) - F_i(N_i, N_j).$$

and the condition of each population as denoted by its weight (w_i) as governed by

$$\dot{w}(K_i, N_i) = E(K_i, N_j) - m_i(N_i, w_i, s)$$

Here the changes in a population in time (t) depicted by the dot over the variables depend on the spatial changes in the distribution of organisms, i.e. passive advection by ocean currents and direct swimming. This derivative can further be expanded into a mean swimming or advection component and a stochastic, turbulent portion tied to random variations in swimming and the inherent contribution of oceanic flows. The importance of the spatial context is manifest in the spatial/temporal distributions of carrying capacity K_i, N_j and the mortality (μ_i), foraging, and metabolic functions E, s, m_i. The latter are typically strong functions of environmental variables

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such as temperature (T) or salinity (S) making the population dynamics dependent on fluctuations in the physical climate. The foraging function involves competition within a population and with others (N_j). The metabolism of the population is dependent on its total mass ($N_i w_i$) and a measure of their activity level, s. Mortality in the population equation is divided into natural mortality, μ_i, which depends on the metabolic status of the population and predation by N_j. The metabolic dependence links the population and metabolic equations while the populations in a region interact through direct predation and competition for resources in the metabolic equation. Finally, there is mortality imposed by fisheries, F. In Fig. 1 fishing is only imposed on the highest trophic level, but the system can be generalized to include multiple fisheries or mortality due to bycatch on lower trophic levels as seen below.

Before moving on to some examples of using the system above it is worthwhile to consider general approaches that might be taken in analyzing them. Given a much better understanding of marine ecosystems than we currently have one could picture a large simulation model that uses this system or one like it to understand and eventually even forecast species interactions under the impact of fisheries. Here the emphasis is on two issues necessary for making the system more complete. The first is the formulation of the functions in the equations above. The second involves setting up trial systems that allow concrete analysis of the system. By carrying out these exercises the model system and our understanding of the marine ecosystems and the part of fisheries within them will be improved. At the same time efforts to understand and apply systems such as the one above can act as an important means of developing new hypotheses and designing new fieldwork.

Nonlinear mortality: starvation

As an example illustrating the formulation of the functions above, consider the natural mortality and its linkage to the metabolism of the population. A common means of parameterizing natural

mortality is to just specify a death rate such that mortality becomes $\mu_o N$. When one considers the distribution of a population in space, however, such a mortality function leads to the conclusion that finite populations will exist in regions where their forage is zero. This is a consequence of the population's exponential decline. While practically one can just assume that a population is effectively zero at some low level, the linear parameterization limits what can be said about the boundaries of a population's range.

Instead consider the linkage between the two equations above when forage is not limiting, i.e. the well-fed state, versus the state where there is no forage. Under the well-fed condition it is possible to find a population equilibrium where there is a steady gain in weight with age. This leads to a steady total biomass when integrating over all age classes. There is still a problem with maximum age, but that is not considered further here. Now, if a well-fed population crosses out of the range of its forage the E term in the equation $\dot{w}$ goes to zero and the population will begin to lose weight as it goes into starvation (Fig. 2). From various considerations ranging from field and laboratory studies of starvation to the basic fluxes that are involved with the biochemical cycles that make up a metabolism, an organism can only withstand a certain amount of weight loss before it will succumb to starvation and die (Walsh, per. comm.). This can be modeled by introducing a formulation for population mortality that depends on the rate of weight loss and is strongly bound as weight drops to some fraction of the maximum weight of the population has attained. Therefore starvation involves burning up a critical amount of the frame that a fish had attained prior to undergoing food deprivation. Without going into the details of the exact formulation used in Fig. 2, the result involves death in a finite amount of time following the onset of starvation as the mortality goes to infinity. The calculation shown in Fig. 2 is only one possible way of paramaterizing starvation. A more accurate formulation would include both total weight as a proxy

for protein and a separate equation for a lipid pool. Such a model could then be used to treat cases such as bluefin tuna and many whale species that undergo long migrations outside regions of adequate forage for reproductive purposes. It is possible to also treat the physiological challenges of such journeys tied to the large changes in environmental temperature and salinity.

Including climate: Metabolic influence of temperature

The model system above also allows the inclusion of the influence of variations of environmental variables on growth and therefore population changes tied to weather and seasonal variations in temperature and salinity. An ability to take these into account is important for understanding the distribution of spawning and recruitment in populations. Accurate treatment of these dependencies, along with their impact on trophic interactions, is also crucial in approaching the dependency of fisheries on short to long-term climate variations. Here only temperature effects are considered.

In this case a model that includes the inherent temperature dependence on growth and development is considered without any food limitation. The simulation is based on an age structured model with exponential increase of growth (increased w) with increased temperature, but with a development rate that decreases with temperature (Fig. 3). The exponential growth with temperature is typical of ectotherms and species such as copepods (Huntley and Lopez, 1991), and cod that are involved in the dynamics of one of history's greatest fisheries (Fig. 4). The reciprocal rate change in the rate of development is important in Calanus finmarchicus and other copepods. This relationship becomes more plastic at higher trophic levels in most phyla. In many phyla temperature also affects the sex ratio in populations at specific age horizons. Here an age-structured model of C. finmarchicus developed in cooperation with Pascual and Davis (per. com.) is used as one example. The model includes an N, w model for C. finmarchicus with 13 age/stage cohorts. The parameters for the metabolic and age development model are derived from laboratory studies. The model is run with

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an annual cycle in the light/nutrient driving for the primary producers. By assumption, these are controlled by grazing from the zooplankton in the model. The model puts the population into diapause (hibernation) from late summer into early winter based on a temperature dependent behavior in the oldest juvenile component's development. The results of an age/stage-structured model for the period from 1982 to 1995 are displayed in Fig. 5. The model despite its nonlinear nature runs to a steady state population given a steady season cycle. Here this involves running the 1982 seasonal temperature for around five years to achieve a steady cycle and then running the model to 1995. The plot shows the diapuased population that sets up the next year's population on Georges Bank. The result shows large interannual variations in populations against an initial condition where the coupled population metabolism model produces a steady cycle given a constant seasonal cycle. The differences between years in Fig. 5 then arise from subtle variations in the onset of seasonal heating and the timing of the onset of the temperature dependent diapause of the population. The level of interannual fluctuations in Fig. 5 is a good approximation to those observed on Georges Bank (Meise-Munns et al., 1990), even though there is not a good year to year match. Exact agreement year by year is not expected given unknown initial conditions and the absence of spatial effects in the model.

In the actual ecosystem of course the copepod population is linked to juvenile cod, which have their own temperature dependent growth rates (Nilseen et al., 1994; Jobling, 1988). While it is not possible to show the total impact on the whole system in Fig. 4, it is reasonable to suggest from the results in Fig. 5 that variations in the physical system's thermodynamics can impact fisheries relevant ecosystems. This dependence on the local water mass properties in time and the inherent movement of populations through advection or active swimming makes it hard to handle the spatial redistribution of populations in the model considered here.

Motion and Spatial Dynamics

There is a growing appreciation for the importance of spatial distributions in ecology (Tilman and Kareiva, 1997), and nowhere is this more important than in marine systems. The importance of movement in almost all marine taxa whether in planktonic, free drifting stages or on the part of large pelagic organisms that can swim across entire ocean basins makes treating these motions in models crucial. The drift of plankton consisting of advection from one site to another by currents or dispersal (diffusion) by ocean eddy fields acts with mortality to produce the distribution of a population around its spawning sites. It is the influence of currents to confine populations in some regions that produces retention of populations in these regions. The behavior of both spawners and newly hatched young can act to enhance or diminish dispersal. Differential movement in response to physical or biotic clues governs contact rates between predator and prey, aggregation of animals along features like fronts, and the formation and function of schools. All of these motions act to determine the spatial structure of a population. Treatment of movement in populations that are also structured with respect to aspects determined by biotic or abiotic conditions encountered in the past becomes a challenge.

The most important point to make in this section is the fact that the population model introduced above is extremely difficult to place in a spatial context in a model with a fixed space or Eulerian description of motion. The problem is the overall complexity of the resulting model that requires the history of a population to be maintained as one moves or mixes across the marine environment (Olson et al., 2001). It is impossible to go into all of the details of models that follow individuals (individual based models, IBMs) or populations advected with water parcels. For examples of carrying out population dynamic simulations in a particle following or Lagrangian frame see Olson and Hood (1994) and the references within. The differences between methods of handling

population movements and their impact near population boundaries may cause significant changes in the results in models. As discussed below this is perhaps the greatest void in our current capabilities. An area that need attention include the response of fish to environmental clues (Humston et al., 2000; Olson, 2002). Aspects of spatial distribution such as schooling (Flierl et al., 1999; Cosner et al, 2000) can change both the response to physical variables including T/S and currents, and the food chain/web dynamics. The influence of motion either due to ocean currents or swimming behavior can be modeled by tracking each individual (individual based model) or estimating the spread of population density or the probability of finding an individual (see Flierl et al., 1999). Finite subpopulations can also be treated on discrete particles instead of using the IBM approach. The use of densities allows the introduction of advection and diffusion operators or the use of transition kernels in integral formulations. Below an example of a Lagrangian, or particle borne population, is given followed by a discussion of a diffusion model.

A Lagrangian model with cannibalism: Alaskan Pollock

The Alaskan pollock (*Theragra chalcogramma*) is a gadiod fish that supports a large commercial fishery in the Bering Sea. The population levels are quite variable in both size and age, structure (Akira et al., 2001) and in total estimated population levels (Bakkala et al., 1987). Causes for this variability are thought to involve climatic shifts in currents, sea ice, and temperature and biotic interactions such as intercohort cannibalism (Wespestad et al., 2000). Here a simple model of the form introduced above is used to explore the impact of predation in an age and spatial structured population (Fig. 6). The pollock are treated as a population of juveniles (J) and an adult population (A). The adults can forage on either J or an alternate prey P. Both J and P are assumed to forage on zooplankton Z. The spatial structures considered include one where the populations are mixed

together and one where the adult population migrates away from the spawning region and only comes back into proximity of the juveniles after a protracted period.

One of the underlying questions here is whether or not cannibalism is a stabilizing or destabilizing factor in population dynamics. One way of approaching this without doing the explicit spatial simulations is to just consider the partition of adult foraging pressure. Given adequate P a modest predation on J actually stabilizes populations in pollock. In the spatial context this is exactly what happens when the adults leave the younger population behind and forage elsewhere for protracted periods. A return to proximity with the J population prior to spawning allows the adults an alternate access to the energy implicit in Z by harvesting their own offspring. The exact details in the model are fairly dependent on the actual growth in J and the amount of resource put into fecundity and production of more J. The model results will also change if more age classes (i.e. more structure) are added. Preliminary considerations of the impact of adding additional age structure suggest that it is stabilizing.

Permanence theories and sustainability

An advantage to considering a fairly low number of interactions among structured populations is the feasibility of formally addressing the degree to which the system will persist over time. This of course involves coexistence of the interacting species through the combined action of the population dynamics and movement in space. Formally the idea is to produce a criterion for permanence in a system so that configurations of species densities starting with finite (positive) populations will remain in some regime where all of the components are bounded away from zero (Cantrell et al., 1993). The formal criteria for permanence typically embody the notion that invasibility, implies coexistence. This means, if each species in a community can increase it's denstiy when introduced at a low density, even with other species already present, then the

community as a whole will persist. Permanence does not require the existence of a stable equilibrium; it allows the possibility of more complicated steady-states, including periodic oscillations or even chaotic dynamics. The key element in permanence is the prediction that densities are eventually bounded away from zero. In particular, the analysis can be applied to spatial models that take into consideration different boundary conditions. For example, in the previous problem on pollock one can consider the difference between a spawning site on a shelf under the condition that J cannot exist offshore under a scenario where they are mixed out to sea versus one where they have a behavioral trait that maintains them on the shelf. This difference in cross shelf boundary condition will clearly change the expectations for the system and is likely to void the criterion for permanence in the non-reflective boundary case, (Fig 7).

The nature of the effects that occur at habitat edges has important implications in the outcome of competition and predator/prey interactions (Fagan et al., 1999). If two habitats and two species are considered as in Fig. 7 a bias in movement or exclusion of one species from one habitat can lead to spatial segregation of the two taxa. This sort of effect can be of considerable relevance to the use of protected habitat areas (Cantrell and Cosner, 1993) where differential influence is tied to variations in the movement of various taxa. In particular the edges in a habitat can produce a condition where species that are not excluded from an area can use it to produce a population surplus that can then out compete the excluded species in smaller protected patches of habitat (Cantrell and Cosner, 1993). The ultimate outcome of setting up a refuge therefore depends on the spatial size, the mobility patterns in the species involved and their inherent population growth rates. Most of the models that have considered these types of problems have used a limited set of taxa. It will be interesting to reconsider these issues with the minimal food-web model introduced above.

In these cases one might expect more complicated behaviors as lack of permanence in some habitats across a region that destabilize food-web dynamics.

Modeling Fisheries Explicitly

In considering the problem of sustainability of fisheries it is crucial that the impact of the fisheries themselves on permanence be directly addressed. In fact one wishes to address the permanence of the fishery effort itself. Here the interaction of two fisheries on a age-structured resource is considered. The fisheries are treated as predators with economic pay-offs in place of metabolic gains. Mortality occurs when pay-offs do not exceed costs. As a thought problem consider the competition between a long-line and a purse seine fishery on an age structured tuna population (Fig. 8). Here if the initial fishery is the long-line fishery targeting larger/older tunas, the question becomes whether or not a purse-seine fleet can successfully invade the fishery. Although it is not commonly thought of in these terms, this is a classic invasibility problem. What are the conditions under which the purse seine fleet can successfully enter the fishery?

Invasibility for F_1 occurs when $\dot{F}_1 > 0$ when $F_1 \approx 0$. A similar criterion applies for F_2. Consider populations $N_1(\hat{F}_1, \hat{F}_2)$ and $N_2(\hat{F}_1, \hat{F}_2)$ where the solutions $\hat{F}_1, \hat{F}_2$ depend on the fish populations and weights. Invasibility for the pristine, unfished situaion in Fig 8 demands

$$E_1[N_1(0,0), w_1(0,0), 0]$$

$$-C_1[N_1(0,0), w_1(0,0), 0] > 0$$

for an F_1 fishery and

$$E_2\big[N_2(0,0),w_2(0,0),0\big]$$

$$-C_2\big[N_2(0,0),w_2(0,0),0\big]>0$$

for a successful F_2 fishery. The deployment of a purse seine fleet F_1 into an existing long line fishery demands

$$E_1\big[N_1(0,\hat{F}_2),w_1(0,\hat{F}_2),0\big]$$

$$-C_1\big[N_1(0,\hat{F}_2),w_1(0,\hat{F}_2),0\big]>0$$

A similar condition exists for the imposition of $F_2>0$ on an existing F_1 fishery.

Under these conditions F_2, the longline fleet, can invade a virgin tuna population as has been seen across most of the tropical ocean. F_1 can also. In the case where F_2 is operational it can also be invaded by F_1. Depending on the detailed parameters involved, this invasion by F_1 may exclude F_2. In the opposite case it is not possible for F_2 to invade or persist once F_1 reaches a given critical size. This is a very simple example, but it illustrates an important point that is at the heart of managing sustainable fisheries from an ecosystem perspective. Namely, that to do this one needs to consider the interaction between trophic levels, the physical environment, and the operating fisheries.

Conclusions

The types of problems posed here and examples discussed are meant to open a dialogue on where modeling can proceed as a useful tool in fisheries. There has been a purposeful choice to keep the models reasonably simple so that there is a possibility to both carry out detailed mathematical analysis and to fully understand the outcome of the various interactions. In this way these models are far simpler than the ECO type models in terms of what species are considered. The detailed biology that can be treated is however more complete. In this way these models provide a tool for

attempting to understand the processes occurring in the ecosystems that produce the populations that ECOPATH treats. While it would be completely naive to suggest that the models here will lead to truly predictive models without a monumental amount of work, they can be used to illustrate important concepts involved with viewing fisheries from an ecosystem perspective. These relatively simple models are also flexible enough to use them as part of the debate on fisheries issues. While there has to be a certain level of "buy-in" on the part of the participants, these types of models are a means of addressing the perceptions various elements have of fisheries. The interactions outlined in the figures above a far easier to convey to a fisherman, for example, than the complicated analysis behind one of the ECO models. At this point in their development the models are also essentially neutral in the sense that allow ideas to be tested without stepping over the line into arguing that they prove anything more than a guide to common sense and a way to explore what is important in a system. Fisherman can then be introduced to the models and the models used to probe their ideas of how different factors effect their fishery. Since the simple structure of the models always allows a level a deniability, if properly used, they provide a learning tool with little threat that they will become an avenue of restrictive management. One can simply state that these simple models are not ready for use in this way.

This brings up the final issue of whether or not a system of models with real predictive skills will eventually arise in fisheries? The authors have to take the tack that they will, and that the approach taken here is destined to play a role. Real predictability of the level seen in modern meteorology forecasts is probably quite a while in the future. It is important to state, however, that the field will not get to a point where real predictions can be made without a much larger investment in data collection, laboratory studies, and modeling from a variety of approaches.

Acknowledgements

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Fig. 1. Schematic of the simplest possible example of a food-web component and the interaction of the upper trophic level with a fishery. The three interacting fish populations are denoted by the N's. The lowest trophic level is supported by a carrying capacity of the environment, K. The interactions of the populations is explicitly assumed be vary as a function of age structure.

Fig. 2. Example of a model of starvation in a metabolic structured population. Here W denotes the weight of the average member of a population. The time period up to ts, the onset of starvation, represents the well-feed state with monotonic weight gain and constant natural mortality. At ts the population is assumed to lose its contact with forage and begin starvation. This leads to weight loss as the population metabolizes body framework, proteins and lipids to maintain itself. This in turn leads to an increase in natural mortality, M, that goes to infinity as the population reaches a lethal fraction, W_i^o, of the maximum attained weight, $W_{i\,max}$.

Fig. 3. Growth rate for calinoid copepods according to Huntley and Lopez (1992) and the envelope of growth for any one species as a function of environmental temperature, T. (McLaren, 1978). The D curve shows the functional shape of development time in copepods in response to temperature. Lower D leads to shorter generation time. The net weight distribution in a population is a trade off between generation time and growth rate.

Fig. 4. Diagram of the copepod model and a schematic of how it might be coupled to a cod population involving juveniles, J, and adults, C. Here P represents a phytoplankton population, e are copepod eggs, Ni the nauplii, Ci the copepedite stages and A the adults. The model here only simulates the copepod response to P and seasonal temperature regimes. Diapause occurs in the C5 stage when environmental temperatures exceed an upper threshold. A more complete system introducing predation by young cod and another fish are shown in the figure, but do not play a role in the simulations shown below.
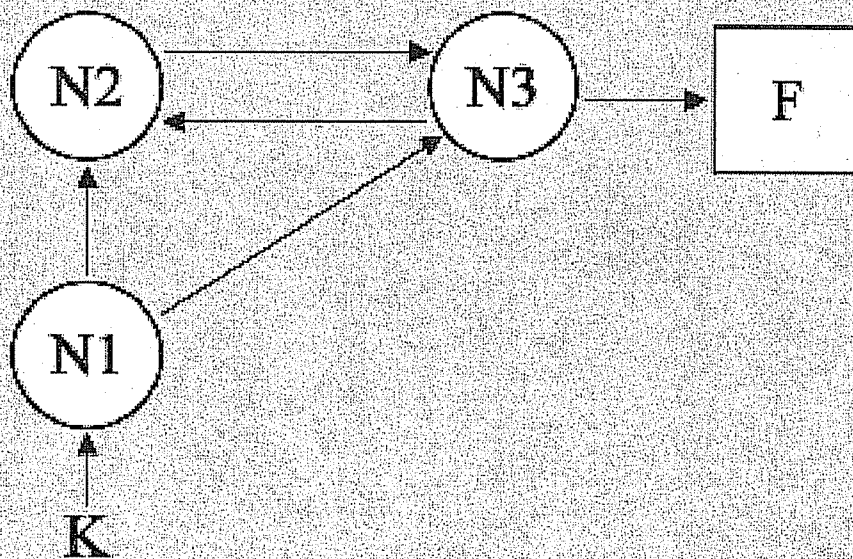
Fig. 5. Sea surface temperature climatology for the top of Georges Bank from 1982 to 1995 and the resulting populations of C5 copepods going into diapause in each summer. Phytoplankton concentration undergo a sharp bloom in each year with the same nutrient light forcing, but with differential grazing depending on the copepod population. The onset of spring in terms of temperature plays and important role in determining both the number of copepod cohorts per spring and their biomass. This in turn modifies the grazing.
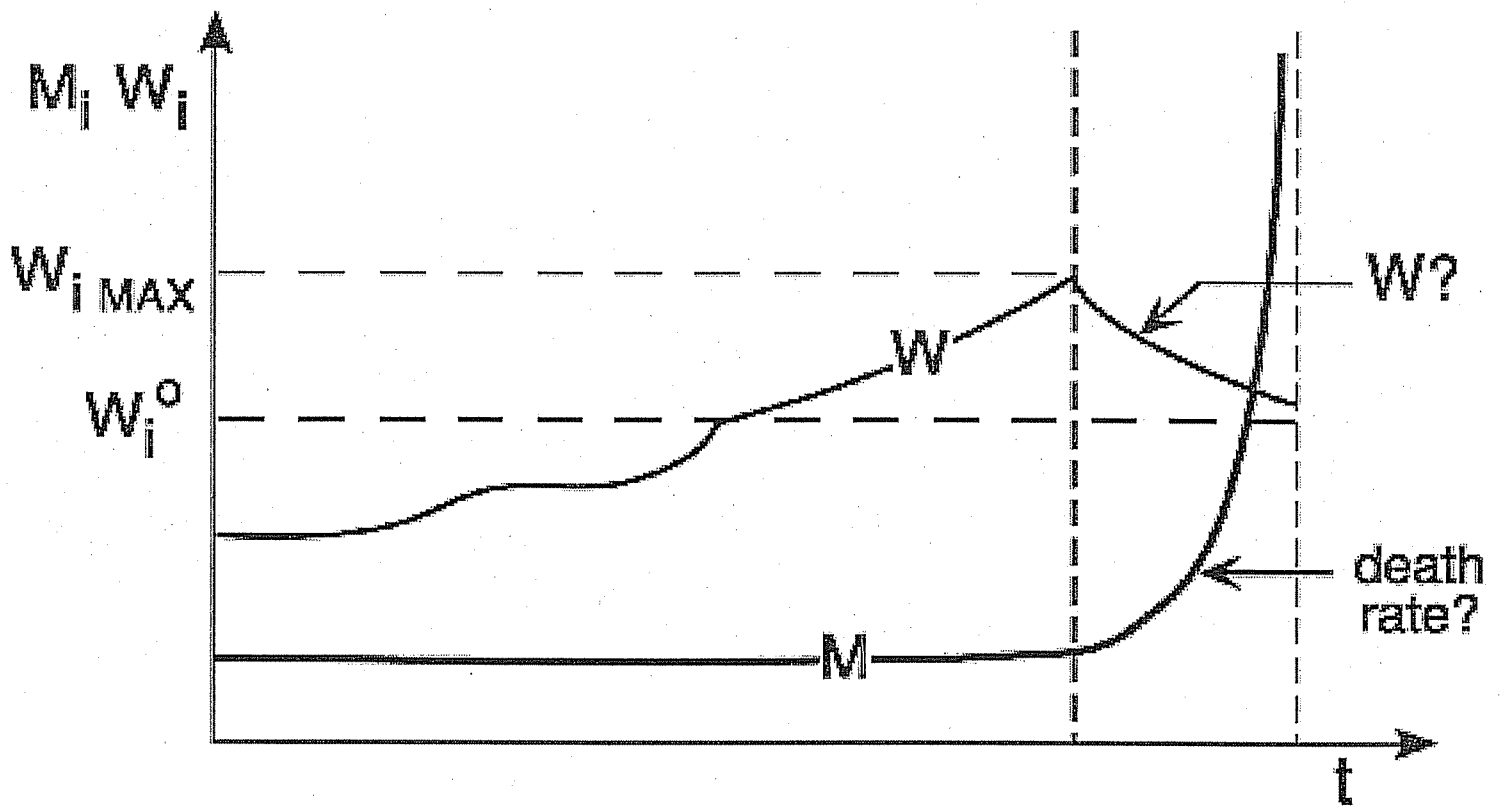
Fig. 6. Schematic of the Bering Sea food-web involving pollock (A), their young (J), an alternate prey for adults (P) and zooplankton (Z). Zooplankton are driven by a carrying capacity. The interaction between A and J involves spawning (dashed line), aging (dotted line) and cannibalism by the adults on the young.

Fig. 7. Diagram of movements across environments and their impact on persistence of populations through the action of conditions at environmental boundaries. Two populations, N1 and N2 are considered between the two regions omega1 and omega2. Several types of motion between regions are considered. These include a biased flux from one region to another as represented by the large versus small arrow at the top of the diagram. The condition where a population does not cross the boundary is represented by the reflecting arrow in the lower portion of the diagram. One of various possible outcomes of these boundary conditions on populations is shown.
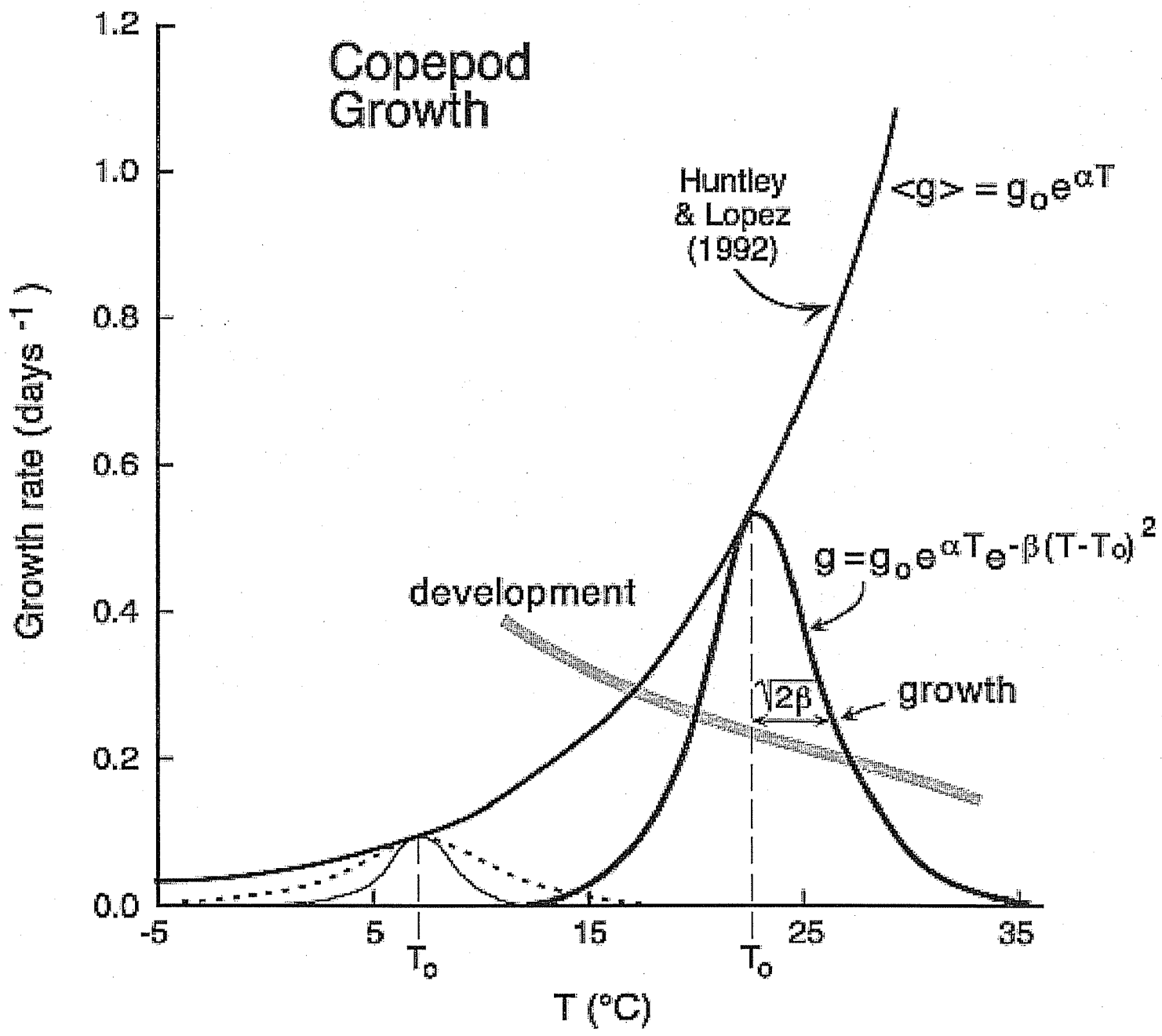
Fig. 8. Diagram of the interaction between an age-structured tuna population (N1, N2) and two fishing fleets (F1, F2). The fNi terms indicate reproduction. The alpha N1 term indicates ageing. The equations for the fisheries are shown below the diagram.

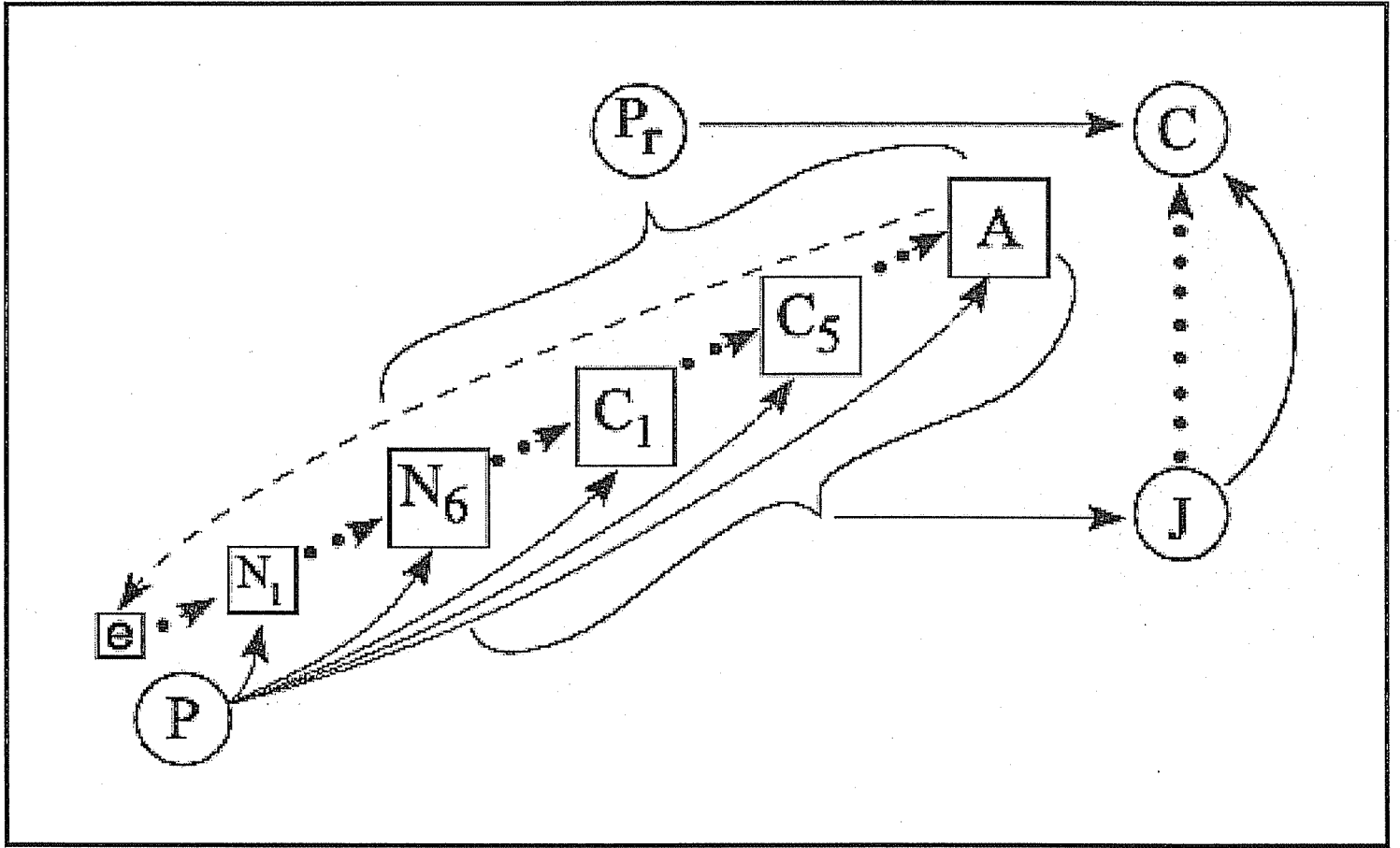Simple Conceptual Model

Copepod Growth

Huntley & Lopez (1992)

$\langle g \rangle = g_o e^{\alpha T}$

$g = g_o e^{\alpha T} e^{-\beta (T-T_o)^2}$

development
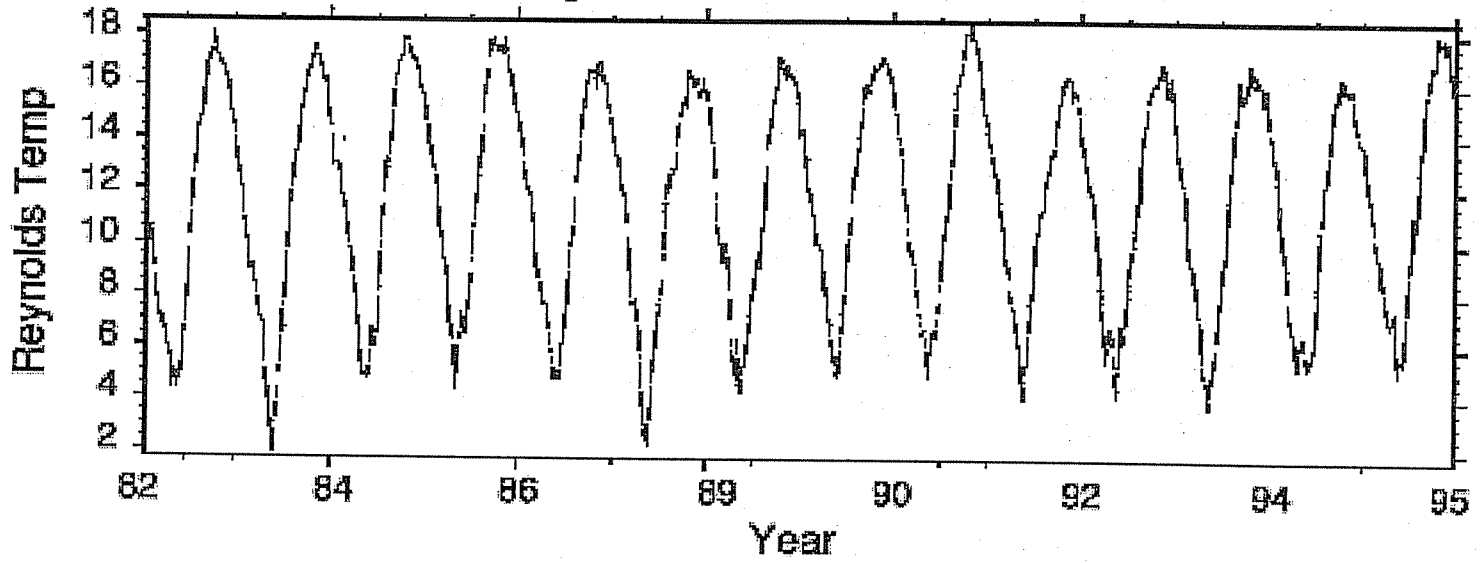
growth

$\sqrt{2\beta}$

T_o

T_o

T (°C)

Growth rate (days^{-1})

Georges Bank: 43° 30'N 67° 30'W

Datafile is /h/mango6/geoff/reynolds/gb.dat

N_1

$N_1 > 0$

$N_1 > 0$

$N_2 > 0$

$N_2 > 0$

Ω_1

Ω_2

$$\overset{\bullet}{F}_1 = \left(\varepsilon_1\left(N_1, W_1, F_1\right) - C_1\left(N_1, W_1, F_1\right)\right) F_1$$

$$\overset{\bullet}{F}_2 = \left(\varepsilon_2\left(N_2, W_2, F_2\right) - C_2\left(N_2, W_2, F_2\right)\right) F_2$$