Successful Surf-Riding on Size Spectra: The Secret of Survival in the Sea [and Discussion]

J. G. Pope, J. G. Shepherd, J. Webb, A. R. D. Stebbing and M. Mangel

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Successful surf-riding on size spectra: the secret of survival in the sea

J. G. POPE, J. G. SHEPHERD AND J. WEBB

Ministry of Agriculture, Fisheries and Food, Directorate of Fisheries Research, Pakefield Road, Lowestoft, Suffolk NR33 0HT, U.K.

SUMMARY

All ecosystems require constituent species to survive against a backcloth of biotic and abiotic scenery. How this scenery shapes the life-history strategies of the players and how they in turn shape the scenery are important themes of the play of life. Species surviving in temperate and Arctic shelf seas do so against a scenery dominated by seasonal changes in the size-spectrum of other players. Successful survival in such an environment requires species to ride the big wave of annual productivity as it rolls through the extended size spectrum from phytoplankton to large fish. This wave flattens and broadens as it moves towards higher sizes.

We speculate that in a seasonal shelf seas environment the wave shape is such that the Sheldon–Sutcliffe spectrum of equal biomass per log size interval is approximately true as an annual average although it may not be true at any particular moment in the year. Such spectra are structured by biomass being moved up the size spectrum mainly by predation processes, with growth of individuals being a second order process. However, the problem for an individual is to grow up through a size spectrum from its size at birth to its size at reproduction. Hence species need to find survival paths through the fluctuating scenery. This scenery is composed of the biomass of the prey, that of animals of a similar size, and larger predators. The paths followed dictate the life-history strategies of the species.

This central problem for sea dwellers in temperate and Arctic shelf seas generates a broad similarity in the choice of life-history strategy for many key players over quite wide geographic areas of the globe. In these seas, strategies of high fecundity, high mortality and high growth rate are particularly common while strategies of low fecundity and parental care are rare for much of the size range. These seas also seem to favour longer trophic chains than terrestrial systems and either several generations per year or multiannual life cycles rather than annual cycles.

1. INTRODUCTION

The ecosystem of the open sea is very different from land-based ecosystems. Most marine primary producers are planktonic and uni-cellular. They are therefore small, and maintain a similar size throughout their short and turbulent lives.

It is upon this substrate of small plant cells that the rest of life in the sea depends. Multi-cellular animals must evolve a strategy for effective utilization of this source of food, and their predators must likewise use them. From these basic factors derives the enormous importance of size as a determinant of survival in the sea.

As a result of this dependence on small plants, life in the sea has evolved a tall pyramid of organisms, spanning perhaps seven or more trophic levels between primary producers and top predators. The textbook terrestrial structure of plant, herbivore and carnivore, is rare as are marine analogues of small animals browsing on large plants or predators of similar sizes to their prey, at least in the planktonic 'mainstream'.

The trophic pyramid in the sea is not only tall, but tangled. The great majority of the animals are carnivorous, and may in principle eat anything of the appropriate size, typically 2 to 3 orders of magnitude less in mass. Because of this cannibalism and cross-predation are common and the potential for interesting and volatile population dynamics is clear!

In temperate and high latitudes, this system is in addition subjected to strong seasonal forcing. Although the classic picture of a spring bloom is not universally applicable, there are many regions, including those which support large and important commercial fisheries, where this is a real and important feature. To deal adequately with these complexities at the species level seems impossible with present methodologies. We are therefore led to consider size structured descriptions of the problem.

The present paper thus follows the path pioneered by Sheldon *et al.* (1972) as it seems to offer the best overview of what is going on in these complex ecosystems. To the Sheldon biomass size spectrum, we add the idea of seasonal variability and develop a simple mathematical cartoon of a seasonally perturbed size spectrum. This describes the great annual wave of production in size-time space, and this sets the

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scenery upon which individual species must play out thier life histories. In what follows we explore, both through illustrative calculations and theory, how species survive on this size spectrum. To survive, they must surf-ride on the wave, growing and reproducing so as to stay abreast of the wave of abundant food of a smaller size, although avoiding the co-evolving wave of predators of larger size. They must be the right size at the right time. The concept of the match–mismatch hypothesis (Cushing 1969) is thus extended to multiple trophic levels and a continuing evolution in size.

2. A BACKGROUND TO SIZE SPECTRA DESCRIPTIONS OF MARINE ECOSYSTEMS

The importance of size as a structuring principle of marine ecosystems was recognized by Sheldon *et al.* (1972, 1973) who observed that pelagic ecosystems appear to exhibit a similar biomass for each log size interval. Platt & Denman (1978) explained this by considering the flux of biomass up the size range which they related to size specific turnover rates and size-based respiration losses. This leads to a steady state biomass spectrum where the biomass in adjacent octaves stand in the ratio of 1.16:1. Platt (1985) reviews the development of thinking on biomass spectra. He concludes that ‘Three principal arguments suggest that the biomass spectrum has an important future in marine ecology’. These he gives as it being: (i) ‘an operationally viable, alternative taxonomy’; (ii) ‘it lends itself to determination by automatic devices’; and (iii) ‘it contains latent information about community metabolism’. A recent compendium of work on this subject can be found in Paranjape & Sheldon (1991).

Biomass spectrum approaches have also found a place in discussions of the nature and exploitation potential of the larger (demersal fish) components of the size range. They have been shown to be conservative features of systems and useful comparative tools for the North Sea, Faeroe Bank and Georges Bank (Pope & Knights 1981; Anon 1988; Pope *et al.* 1988).

Silvert & Platt (1978) show how the theoretical description of a biomass spectrum can be extended to a simple time dependent model. Their model implies that a discrete perturbation would propagate up the size spectrum with unchanged shape but with an amplitude that diminished in the same ratio as that of the steady state spectrum. They note that in reality they would expect the perturbation to be smeared out and flattened as it increased in size due to feedbacks not included in their model. In a further paper (Silvert & Platt 1980), they extend the theory and derive and discuss several forms of the dynamic equation. Unfortunately, except in steady state conditions, solutions of their equation seem elusive.

The existence a systematic size spectrum has implications for mortality and for growth rate at size. These were used by Beyer (1989) to develop an equation for survivorship over a weight range $(w_1–w_2)$ as,

$$(w_2/w_1)^{-z/g}, \tag{1}$$

where z and g are the coefficients of mortality and growth in his equations. Hence biomass $b(w_2)$ at a given size w_2 will be given by

$$b(w_2)/b(w_1) = (w_2/w_1)^{(1-z/g)}. \tag{2}$$

If $z < g$ this implies that a given investment in biomass at size w_1 will give a biomass at w_2 that will increase if w_2/w_1 is larger. Thus biomass growth to a given size w_2 will be greater if the initial size w_1 is smaller. This would explain why many fish species tend to produce eggs of a small size. Ware (1975), considered the optimal size of fish eggs and concluded they should be small. His model also explains the observation that larger eggs are produced in the colder winter months by some species and therefore accounts for some seasonal changes in the optimal spawning behaviour. However, it does not explicitly consider the seasonal changes in abundance of suitable sized prey or predators.

3. MODELLING GROWTH AND MORTALITY IN A SEASONAL SIZE SPECTRUM

In this section we develop a simple model that concentrates on the seasonal changes in the predator and prey scenery and initially ignores changes in the abiotic environment such as light, wind mixing and temperature. Our justification for the omission is to enable us to simply describe the main effects of the biotic environment on cohort survival. The seasonal model could thus be seen as an attempt to extend the Cushing match–mismatch hypothesis (Cushing 1969), to a more general ecosystem description. Here we conjecture that the seasonal size spectrum: (i) would approximate to the Sheldon spectrum if averaged over the annual cycle; and (ii) would exhibit seasonal patterns with large amplitudes at small sizes that would become progressively damped and retarded towards the larger end of the size spectrum. As a template for the relative abundance function at log size and time $B(a,t)$, we choose, somewhat arbitrarily, the von Mises (probability) function:

$$f(r,t) = \frac{1}{2\pi I_0(r)} \exp\left[r \cos\left(2\pi \frac{t - t_0}{52} \right) \right], \tag{3}$$

where the time t is measured in weeks. This function has a single peak at $t = t_0$ whose height and width is controlled by the parameter r. The function $I_0(r)$ in the normalization factor is a modified Bessel function of the first kind and order zero. In passing we note that this function has several attractive features. In particular the products and ratios of two different von Mises functions also have the shape of a von Mises function. It also has the property

$$\int_0^{52} B(r,t)\,\mathrm{d}t = 1. \tag{4}$$

This can be used to embody the Sheldon hypothesis of equal biomass per logarithmic size interval when the biomass spectrum is integrated over a year.

We postulate that r decreases and that t_0 increases linearly with the logarithm of relative size a, where $a = \ln(w/w_0)$, and w_0 is some reference mass. We thus

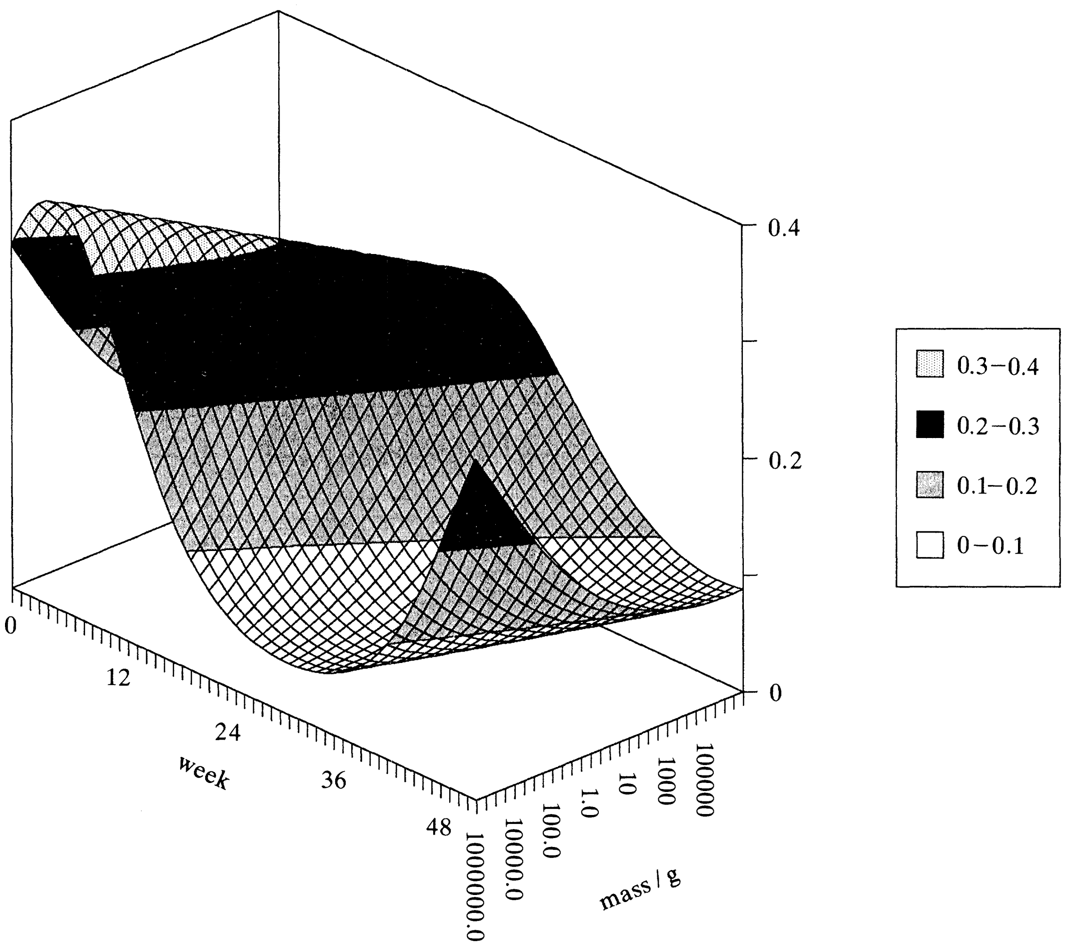

Figure 1. The relative biomass at size spectrum adopted in the simple model.

describe the relative abundance of organisms of size at time t by a function $B(a,t)$

$$B(a,t) = \frac{1}{2\pi I_0(m-\eta a)} \exp\left[(m-\eta a)\cos\left(2\pi\frac{t-ka-d}{52}\right)\right], \quad (5)$$

that, with appropriate choices for the parameters m, η, k and d, would have these features. Figure 1 shows the shape of the relative biomass spectrum adopted in our model. Small organisms (phytoplankton) have a considerably narrower and peakier distribution than the large fish.

Having described the stage scenery we can consider the actors. Standard equations for describing growth and mortality (Beyer 1989) are

$$\mathrm{d}w/\mathrm{d}t = g_0 w^{1-m},$$

$$\mathrm{d}n/\mathrm{d}t = -z_0 n w^{-m}, \quad (6)$$

where the constant m is usually taken to be in the range 0.23 to 0.28 derived from Fenchel (1974). The seasonal model modifies these equations so that the constants g_0 and z_0 become periodic functions of time to represent seasonal changes in growth and mortality which result from seasonal fluctuations in the abundance of predators and prey. The equations then become

$$\mathrm{d}w/\mathrm{d}t = gB(a-\varrho,t)w^{1-m},$$

$$\mathrm{d}n/\mathrm{d}t = -zB(a+\varrho,t)nw^{-m}, \quad (7)$$

where

$$\varrho = \ln\left(\frac{w_{\text{predator}}}{w_{\text{prey}}}\right). \quad (8)$$

As an illustration of the seasonal model we consider the growth and mortality of fish larvae in the first year of life. Model parameters were chosen to be compatible with the growth and mortality of North Sea cod over their first year.

Simulations with different starting dates provide growth trajectories in the size-time plane; these are illustrated in figure 2. Progression through the size range is clearly different for different starting dates, later trajectories having markedly lower growth at smaller sizes. The mortality rates and cohort numbers for each of these trajectories were calculated and the biomass changes associated with each trajectory derived. These are shown in figure 3 and indicate that the optimal trajectories start in advance of the wave front. This is because annual gains in mass do not appear substantially different between trajectories (37% difference) but the mortality rates for the later trajectories are systematically higher and the resulting population numbers after a year differ by two orders of magnitude between the best and worst trajectories. Hence biomass changes over the first year range between plus or minus an order of magnitude.

Clearly a suitable choice of timing allows the 'cod' cohort to traverse the seasonal size spectrum in a way

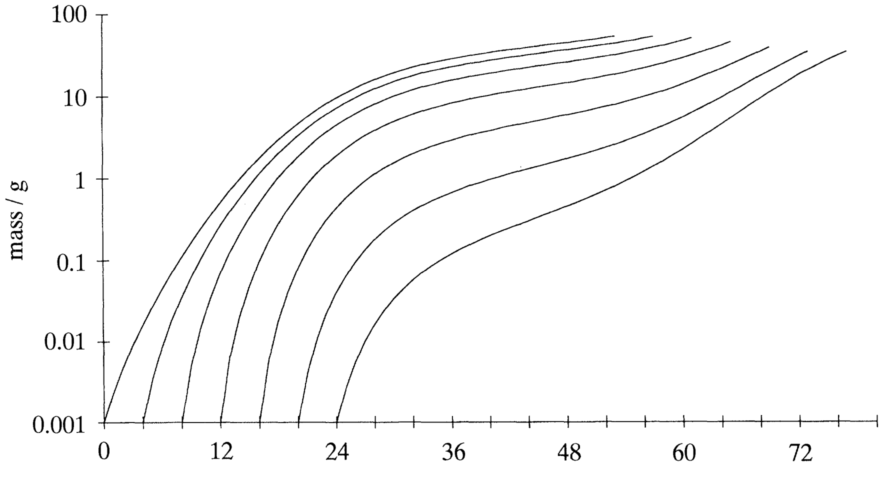

Figure 2. Possible growth trajectories for a larval fish, 'cod', in its first year of life resulting from different starting dates.

that enhances its biomass. Inspection of the biomass curves indicates that biomass decays at some time on all curves. This is of course occurring when the young fish have to pass the food minimum and the biomass peak of their predators as it is a consequence of the model formulation that no fish can ultimately grow fast enough to stay ahead of these. The best solution therefore seems to be to pass through at the largest practical size and the optimal 'fish' strategy is to start life in advance of the prey wave and thus to stay in front of the predator wave for as long as possible.

We may also use the model with the same parameters to investigate possible growth curves for a copepod (assuming for convenience that this has continuous rather than staged growth). Unlike a cod a copepod will have a maximum size that will occur during the year. Using initial and final sizes based upon *Calanus finmarchicus* and using model parameters as for cod, we derive the growth curves and the resulting biomass curves, shown in figure 4. These again show the benefit of sensible egg timing and of the desirability of passing the predator wave at the largest possible size. Copepods grow rapidly to their final size on the trajectories which start before the prey peak (n.b. the kink in the biomass curves is where they reach final size). After the prey peak they slow down. Mortality rates are generally higher after the prey peak. The combination of growth and mortality gives biomass increases of one to two orders of magnitude on the trajectories which begin at or before the prey peak. However, trajectories which start after the prey peak show biomass losses of as much as six order of magnitude. The rapid early growth might give some copepods adopting an early trajectory the opportunity to spawn eggs into the same prey wave as they were spawned in and to take a second biomass growth dividend from this wave. Spawning outside the wave would however lead to rapid loss of biomass of the spawned cohort. It would therefore seem more efficient to maintain biomass as adults and to ride out the time of low growth and high mortality at the adult size. Given the levels of mortality on the adults it might also be efficient to seek to avoid this by moving to areas lower food and lower mortality rate.

These two examples illustrate the main features of the seasonal model. It is, however, possible to genera-

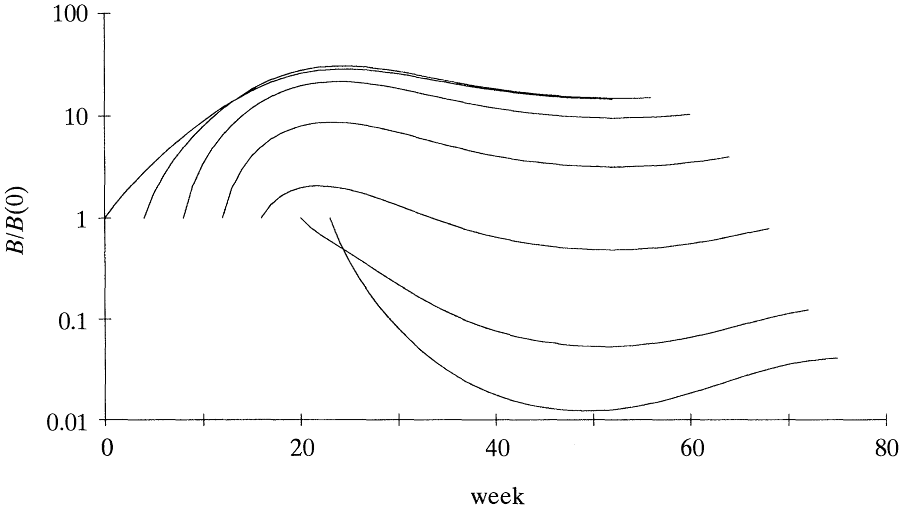

Figure 3. Biomass changes for 'cod' cohorts growing on trajectories with different starting dates.

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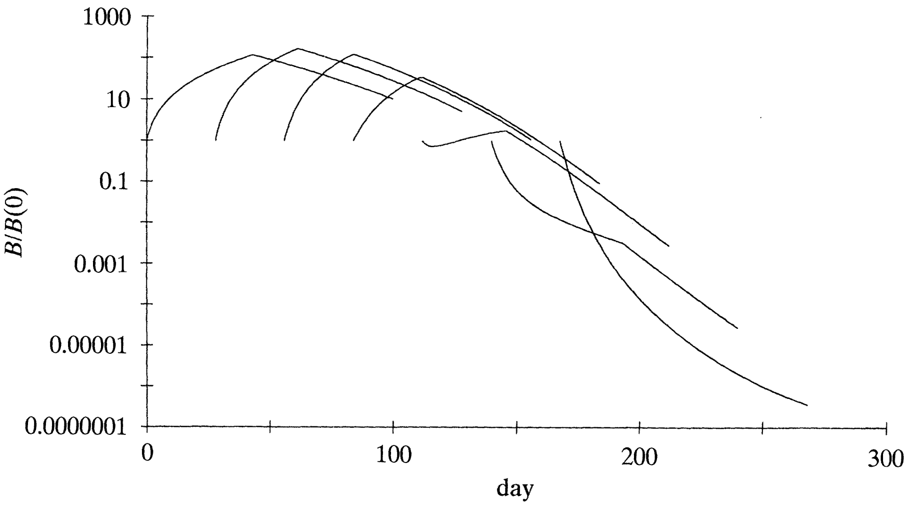

Figure 4. Biomass changes for 'copepod' cohorts growing on trajectories with different start dates. The discontinuity in gradient on these curves results from growth ceasing at the maximum size.

lize further. Equation (7) proposes a growth rate dependent only on size and time. We may therefore draw a series of growth trajectories across the time-size plane. These would look like those shown in figure 2 but would span the entire size range. Individual species may use sectors of these trajectories. For example, cod may start at a size of about 1 mg on a trajectory whereas a copepod may stop growing at this size and an elasmobranch may start on a trajectory at a mass above 1 g. Equation (2) gives the gain in biomass from growing from mass w_1 to mass w_2. In the seasonal model the ratio of z to g, at any time and size, is the ratio of two separate von Mises distribution. This forms a new (non-normalized) von Mises distribution with a new lag and multiplier. The new distribution is of the form:

$$\frac{z(a,t)}{g(a,t)} = \frac{I_0(m-\eta(a-\varrho))}{I_0(m-\eta(a+\varrho))}\exp\left[\varpi\cos\left(2\pi\frac{t-ka-\lambda}{52}\right)\right], \quad (9)$$

where

$$\varpi = +\left(\left(2\eta p\cos\left(\frac{2\pi\, kp}{52}\right)\right)^2 + \left(2(m-\eta a)\sin\left(\frac{2\pi\, kp}{52}\right)\right)^2\right)^{0.5}, \quad (10)$$

and

$$\lambda = \frac{52}{2\pi}\left(\pi - \tan^{-1}\left(\left(\frac{m-\eta\, a}{\eta\rho}\right)\tan\left(\frac{2\pi\, k\, \rho}{52}\right)\right)\right). \quad (11)$$

Equation (9) will range between below and above 1 and it follows that for a particular mass the biomass growth per logarithmic size stage (see equation 2) is positive at some time in the year and negative at some other time. Because we would expect η to be small ($\ll 1/\varrho$) the most negative periods of biomass growth per stage occur at a time somewhat less than half a year after the prey peak. Figure 5 shows the plot of $1-z(a,t)/g(a,t)$ in a size-time plot. This indicates the sizes and times for which biomass growth will be negative. Because both logarithmic stage growth and the losses caused by the $1-z(a,t)/g(a,t)$ term are lower at larger sizes, the obvious strategy for traversing the period of negative biomass growth would seem to be to do so at the maximum possible size.

Equation (2) also implies that the logarithmic species biomass change between time t_s and t_f is given by

$$\ln\left(\frac{B(a(t_f),t_f)}{B(a(t_s),t_s)}\right) = \sum_{a(t_s)}^{a(t_f)}\left(1-\frac{z(a,t(a))}{g(a,t(a))}\right). \quad (12)$$

If the various growth trajectories are plotted on axes of size and the $(1-z(a,t)/g(a,t))$ value, then the average level of equation (12) on a section of trajectory can be readily visualized. Figure 6 shows such a plot. Sections of trajectories with a positive average represent biomass enhancing strategies whereas those with negative averages represent biomass losing strategies. Notice that none, if ridden for the full year, is entirely negative or entirely positive but that some are positive for more size bands than others. It is also worth noting that some of the latter trajectories, that would be disastrous for fish larvae to follow, begin to have positive values of $(1-z/g)$ at sizes greater than 1 g. Thus they might be sensible trajectories for the young elasmobrachii that start life at about this size. If species have multiple generations per year the appropriate response would seem to be to mature rapidly and to put eggs onto a following trajectory that is still contained in the prey peak in which the parents were born. Once this passes and the predator peak approaches it would be more efficient to conserve biomass as adults and to wait for the next wave.

These diagrams therefore illustrate the central problem of living in a seasonal biomass size spectrum. Paradoxically, the best way of utilizing the prey peak is to do so at as small a size as possible but the best way of avoiding losses during the prey trough–predator peak is to do so at the largest size possible. It is therefore the business of marine species to find robust trajectories between the horns of this dilemma.

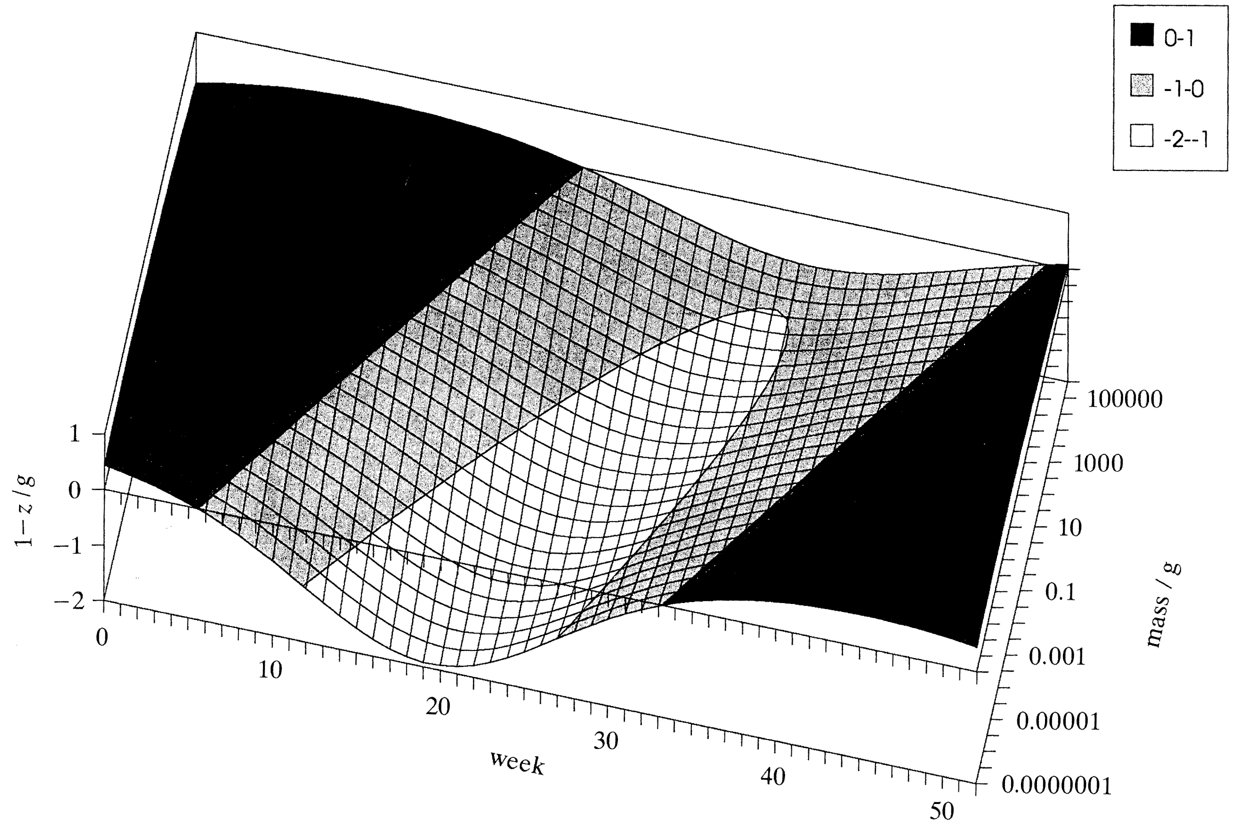

Figure 5. The $(1-z/g)$ surface in size time.

The modification of both growth and mortality by ambient temperature has not so far been implicitly addressed in the model. Because the seasonal cycle of temperature can clearly produce modifications in growth and mortality this process needs to be addressed. If temperature effects modify the coefficients of growth and mortality equally, then the $1-z/g$ values will remain unchanged but growth trajectories will change. Because prey trough–predator peaks will tend to occur at warmer times of year the general effect of this effect may be to amplify the problem of passing the predator peak with minimum biomass loss. The annual temperature cycle may be included in the model by modelling temperature change as an additional von Mises function. If temperature (T) enters the growth and mortality coefficients in the form T^x then the multiplicative property of von Mises functions ensures that the seasonal growth and mortality modifiers still follow von Mises distributions. Thus while the form that size enters these new distributions

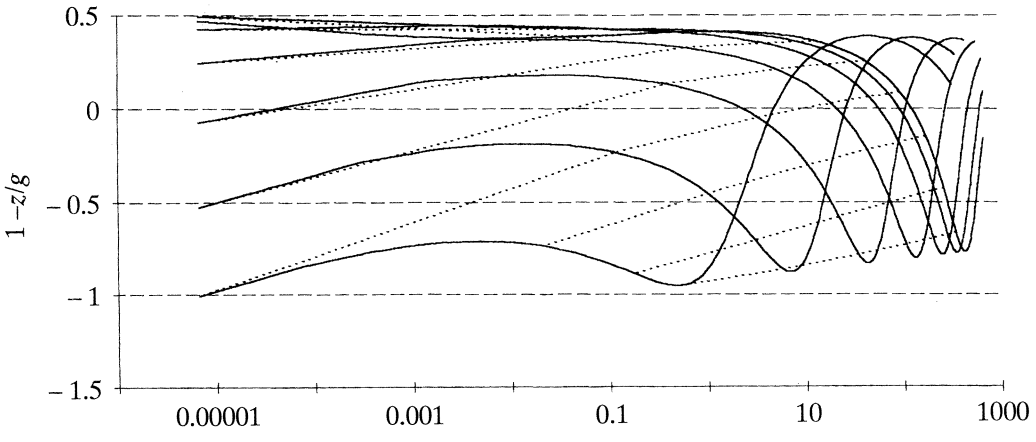

Figure 6. The strategy space diagram. Growth trajectories (solid lines) are plotted on log size and on the value of $(1-z/g)$. The average value of $(1-z/g)$ over a sector indicates the biomass gain or loss to be made (see text). Contours of equal time are also shown. Positive values of $(1-z/g)$ lead to biomass increases whereas negative values lead to declines.

is more complicated the broad consequences of a seasonal size spectrum illustrated above still seem to hold.

DISCUSSION

The seasonal nature of events in the temperate and Arctic shelf seas has been appreciated from the earliest times. We conjecture that the resulting size-time biomass spectrum would average over a year (and over space) to the form similar to that proposed by Sheldon *et al.* (1972). We are not aware that this conjecture has yet been tested by a systematic study of a whole area for a whole year. However Sprules *et al.* (1991), shows the size spectrum of two different times of year for Lake Michigan and Hargrave *et al.* (1985) show seasonal size spectra for one station in the southern Gulf of St Lawrence.

The speculative seasonal size spectrum model presented is an attempt at a simple mathematical description of the seasonal biotic environment. Thus the functional form was chosen as a simple cartoon of a seasonally varying biomass spectrum rather than as a solution to one of the Silvert & Platt (1980) formulations of the master equations. Clearly it should be further examined to see if either it seriously violates the biological constraints of the system or if the equation provides some conditions on the parameter set.

In its present form it does provide some insights into the problems of living in the seasonally size-structured environment of the sea. These insights are not seriously affected by the precise formulation of the model but result from both the succession of good and bad feeding conditions and the phase shift between these and predation pressure. The existence of these phase shifts is supported by observation (Sprules *et al.* 1991; Brander & Hurley 1992).

Life in a seasonal system can be illustrated by considering the fate of some species. These illustrate the substantial gain to be achieved by the right timing strategy and the losses that may be incurred by the wrong choice. Thus marine dwellers face the dilemma that it is good to be as small as possible, to take advantage of the potential for biomass increase in the growth season, but it is bad to be small when the seasonal food supply is reduced and when predation pressure is increased. The obvious strategy is to 'surf' up the size distribution, riding the prey wave as long as possible and staying ahead of the predator wave as long as possible. Alternative strategies adopted find ways of avoiding the worst aspects of small size.

The efficiency of some strategies may depend upon the extent to which reduced mortality can be bought at the expense of reduced growth. This may be a critical question. It is certainly possible that active searchers for food may concomitantly increase their contact rates with predators (Gerritsen & Strickler 1977), or that some systems or parts of systems may have higher densities of predators and prey and hence higher vital rates. Comparison of observed mortalities on fish eggs, and on newly hatched larvae, reviewed in Pepin (1991) lead him to support the linkage between growth and mortality but indicate that, at least for fish eggs, not growing does not eliminate mortality rates. Fish eggs may not be the ideal example since the risks to eggs, of being in a high mortality but productive area, may be balanced by the growth to be anticipated later. A true mortality avoider might have a wider range of strategies to choose from (e.g. moving into less productive regions) and more means to achieve them than the limited repertoire of an egg.

An alternative general strategy of avoiding small egg sizes and joining the size spectrum at a larger size and later date is adopted by the elasmobranchii. The simple model suggests that this behaviour corresponds to exploiting another maximum in the strategy surface. A somewhat similar strategy is adopted by salmonids in their marine phase. The strategy of being large relative to food requirements is adopted by gelatinous zooplankton. This seems superficially such an elegant solution for coping with size related mortality that there must be some drawback to prevent its universal adoption. Turbulence might be one such limit (T. Osborne, personal communication).

This simple model suggests that repeated spawnings on to the same prey wave could be a profitable strategy for small fast growing animals such as copepods. Spawning outside of the prey wave peak would however be inefficient and lead to loss of biomass. Thus animals have the choice to be small repeat spawners for part of the year or to move on to an annual or multiannual spawning cycle. In principle a true annual cycle would seem advantageous as it would benefit most from the potential for high biomass increase at small size. Despite this annual spawn and die cycles seem to be the exception for temperate and Arctic fish species. Studies of the strategies of planktonic organisms which are annual spawners may shed some light on this problem.

A further feature of the structure of marine ecosystems that may be influenced by the need to adapt to a seasonal size spectrum is the large predator to prey mass ratio common in the pelagic food chain. Closer predator–prey size ratios are seen in demersal fish (Ursin 1973; Rice *et al.* 1991). Hence for fish, at least, the size ratio does not result from a physical limitation. An explanation might lie in the variation in the amplitude of the seasonal cycle with size. If, as proposed in the seasonal model, the amplitude of the cycle is a decreasing function of size then it may pay to reach as far down the size spectrum as possible to take advantage of the higher amplitude of the cycle of smaller size groups.

The simple seasonal model proposed clearly lacks many of the features found in real ecosystems. The model formulation adopted does not explicitly consider the effects of seasonally changing non-biotic factors. However, it has been indicated that a seasonal modifier of growth and mortality (e.g. temperature) might be described approximately by a von Mises distribution. Hence its product with the simple model would modify the simple model but not change its essential character.

Another obvious deficiency of the existing model is the lack of spatial patchiness. It would be possible to consider an extension of the model, where several spatial cells at one size level were integrated as the prey of the next size level. The properties of such a model would depend upon the phase and amplitude shifts in the seasonal biomass size spectra in the integrated cells. We suspect that the existing model captures the main aspects of life in a seasonal marine environment where riding the wave of prey biomass is the secret to survival in the sea.

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Discussion

A. R. D. Stebbing (*Plymouth Marine Laboratory, Plymouth, U.K.*). There is an adaptive change in size spectrum which I demonstrate in benthic hydroids (*Laomedea flexuosa*) which is of interest here. In response to different types of stress (e.g. toxic metals, sub-optimal salinity) in experimental cultures, growth is diverted from asexual growth of sessile colonies to the production of planktonic medusae. In the environment this can be interpreted as an escape strategy from conditions unfavourable to the adult colonies. There are published data that indicate that the reciprocal strategy of escaping from the water column by accelerated metamorphosis may also be true, because it has been shown experimentally that the development of planktonic larvae may be more rapid in response to toxic agents.

J. G. Pope. This is an interesting point and suggests that gelatinous zooplankton are even more sneaky than we realized! In the discussion it was noted that their place in the size spectrum is interesting. Should they be included according to their physical size or according to their energy content and requirements? By being physically bigger than their physiological place in the size spectrum they seem to have found a rather neat way of exploiting it. If, in addition, some can move between life styles when conditions become adverse then we are even more puzzled to know why they have not taken over the world. As we asked at the meeting, 'what is the drawback to being a gelatinous zooplankton'?

M. Mangel (*Section of Evolution and Ecology, University of California, Davis, California, U.S.A.*). At the end of the talk, the authors asked 'Why are there no annual fishes?' I believe that the answer is, at least in part, there would be if they could. Given ideal physiological conditions, fish will mature and reproduce at the earliest opportunities (Thorpe 1991, and references cited therein). As Thorpe has argued, to fully understand this question, we must focus on the developmental program, which is genetically determined, as it interacts with the environment. Perhaps it would be better to ask 'What in the environment limits fish from regularly reproducing in the first year of life?' In the verbal discussion following the paper, it was pointed out that many squid are 'annuals'. The difference between fish and squid could be the production and maintenance of the skeleton and that this investment by fish causes, in general, a delay of reproduction and iteroparity.

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R. J. H. Beverton (*Emeritus Professor of Fisheries Ecology in the University of Wales College of Cardiff, U.K.*). Herring may be a good test of the authors' surf-riding hypothesis, because one or more of the many local populations around the North Atlantic fringe can be found which spawn in each month of the year. It seems that the metamorphosis of those that spawn out of synchrony with the plankton 'crest' in that region is slowed down until they pick-up on the next crest. This pattern may be worth more detailed analysis with their methodology.

On a different point, the authors are right that 'annual' fish are uncommon or absent in high latitudes. However, the smaller species of squid are strict annuals and are major components of high-latitude ecosystems. Have they tried their ideas on them?

J. G. Pope. Both Professor Mangel and Professor Beverton point out that squid seem to succeed in being annuals in temperate and Arctic systems when fish generally are not. We note that some small temperate fish species are annuals, e.g. the gobies, but that these seem to favour a non-planktonic spawning behaviour. Professor Mangel suggests that not having the costs of a skeleton might be why squid are annual while most temperate fish are not. We wonder if perhaps another answer might be that because it does not have to ingest whole prey, a squid can progressively move on to relatively larger prey items than a fish can. It could therefore move its predation on to larger and later prey peaks than a comparably sized fish. This would allow it to feed well for longer in its first year and might just give it sufficient scope to be an annual spawner. We believe that Professor Beverton's observations concerning herring might reasonably be explained by firstly suspecting that all these spawnings are timed to local peaks in prey abundance and secondly by remembering that growth and mortality may be modified in the equations by temperatures as well as by prey and predator abundance. The effect of temperature would be to reduce both growth and mortality in the winter. In a system with spring and autumn phytoplankton peaks this would make the 'valley of the shadow' that followed the autumn peak exact a lesser penalty than the valley which follows the spring peak. This might give scope for autumn spawned fish to get away with over wintering at a small size.

J. R. Beddington (*Renewable Resources Assessment Group, Imperial College of Science, Technology and Medicine, London, U.K.*). It would appear that successful 'surf-riders' might be particularly vulnerable to environmental perturbations to prey or exploitation of prey, for example, in an industrial fishery? Is this inference correct?

J. G. Pope. The idea that fish recruitment would be vulnerable to environmental perturbations is of course the central idea of Cushing's match–mismatch hypothesis. Our surf riding story is an extension of this so we would expect the vulnerability to remain. The effect of exploitation of prey, such as sandeel, by small meshed 'industrial' fisheries are less clear. For most species the critical surf ride will have occurred at much smaller sizes of prey than those taken by the industrial fishery. Elasmobranchii or salmonids which enter the marine system at a larger size are perhaps at more risk but even here the size of prey are initially likely to be small than those taken in the fishery. Therefore to have an effect the fishery would have to be causing a reduction in recruitment of species such as sandeels. It is also interesting to note that, in recent studies of sea trout feeding in the North Sea (Ian Russell, personal communication), the small fish seem to be feeding on small clupeoids and only move on to sandeel as they grow larger.