

NOTE AND COMMENT

Patterns and propensities in reproduction and growth of marine fishes

PHILIPPE CURY^{1*} AND DANIEL PAULY^{2†}

¹University of Cape Town, Oceanography Department, 7701 Rondebosch, South Africa

²University of British Columbia, Fisheries Centre, 2204 Main Mall, Vancouver, British Columbia Canada V6T 1Z4

A number of strong regularities characterize certain very basic biological parameters in marine fishes. For example, the ovulated eggs of fish usually measure approximately 1 mm in diameter. The small, relatively uniform size of the eggs means that almost all fish larvae experience environmental variability at very similar scales, which itself establishes strong constraints for, and links between reproduction and recruitment. Additional constraints emerge from seawater being a poor medium for respiration, which establishes further linkages between growth and mortality. These constraints have produced strongly convergent features, and thence the patterns in reproduction and growth of marine fishes that are presented.

Key words: comparative ecology; growth; marine fish; patterns; reproduction.

INTRODUCTION

Science in general, and ecology in particular, often proceed from the identification of patterns or propensities to the construction of theories, then back to the detailed analysis of the patterns, toward the development of more powerful theories (Peters 1992; Levin 1993), or the quantification of the propensities (Popper 1996). Thus, pattern recognition and explanation of the related propensities are keys to increasing ecological knowledge (Bakun 1996; Popper 1996). As advocated by Bascompte and Solé (1998), referring to spatio-temporal patterns in nature, 'new stages in our understanding of ecological processes can only arise from a fertile interaction between theory and data'. However, questions may arise concerning the ubiquity of patterns, especially whether the same

basic patterns occur in both terrestrial and marine environments.

Even though the ocean and atmosphere share the same basic fluid dynamics, strong differences in mean density and viscosity are observed (Steele 1995). The sea consists of a fluid medium, and turbulent diffusion acts as the main dispersive mechanism for small organisms, which live in a three-dimensional environment; viscosity is a major constraint but gravity is not important. Furthermore, there is very little oxygen dissolved in even the best-aerated water, as compared with the O₂ content of air. Because of inertia in the marine environment, sea temperature is much more predictable, even at small scales, than air temperature; overall, the ocean is less variable or 'noisy' than the atmosphere (Steele 1985, 1995).

These features have important implications for the life-history of marine organisms, and we shall illustrate these using three examples of linked adaptations generated by these features, and involving the basis of life-history. The links between reproduction and recruitment in relation to the physical environment, between growth and respiration, and between mortality and growth

*Email: pcury@sfrl.wcape.gov.za or curypm@uctvms.uct.ac.za

†Email: pauly@fisheries.com

Received 1 July 1999.

Accepted 24 August 1999.

will be presented. Even though these examples are not explicitly linked, they depict the existence of strong patterns and regularities that can be observed in marine ecology.

Existence of an optimal environmental window for fish recruitment

With few exceptions, the ovulated eggs of fish usually measure approximately 1 mm in diameter irrespective of the size of the adults (Fig. 1). The relatively uniform small egg-sizes imply that nearly all fish larvae may experience environmental variability at very similar scales. Furthermore, as adult fishes tend to be very large relative to their eggs, most fish species produce orders of magnitude more eggs and larvae than are needed for replacement. The vast majority of these eggs and larvae die within a few days, and individuals that do survive to a more advanced stage (usually well past metamorphosis and settlement in the case of demersal species) are referred to as 'recruits'.

Food availability and physical constraints, such as turbulence, are now considered to be the key factors affecting larval survival and subsequent recruitment (Bakun 1996; Cushing 1996), although other factors, such as predation, also appear to play an important role in larval survival (Chambers 1997). Food availability for larvae is enhanced by wind-induced mixing, which increases primary production, up to a point where the biological processes are disturbed by turbulence. Consequently, the relationship between

pelagic fish recruitment and wind intensity, at least in upwelling areas, tends to be dome-shaped (Cury & Roy 1989; Cury *et al.* 1995; Serra *et al.* 1998); recruitment increases with upwelling intensity until wind speed reaches a value of approximately $5\text{--}6\text{ m s}^{-1}$, creating an optimal environmental window for recruitment (Fig. 2). Some turbulence, because it increases the encounter rate between food particles and larvae, may be beneficial to larval survival. However, intense wind-driven turbulent mixing that disaggregates patches of larval food is detrimental. Also, wind-driven turbulent mixing is associated with strong offshore transport, which displaces larvae from favorable coastal areas.

Given that most fish species have larvae similar in size to those of pelagic species that are abundant in upwelling systems, optimal conditions for the survival of fish larvae in general should correspond to wind intensities of $5\text{--}6\text{ m s}^{-1}$. As it turns out, this is approximately the average wind speed above which wind stress begins to exert a measurable mixing effect on the surface layer of the near-shore water (Kullenberg 1978), and also the threshold value above which wind mixing tends to disaggregate phytoplankton patchiness (Therriault & Platt 1981). This range of wind values also defines the spatial and temporal windows for pelagic fish reproduction in upwelling zones (Shin *et al.* 1998).

Selective pressures have strongly shaped reproductive life-history traits such as egg-size and therefore patterns between fish recruitment (the dome-shaped relationship of the optimal environmental window) or the spatial fish reproductive strategy coupled with the environment appear to be consistent between fish species.

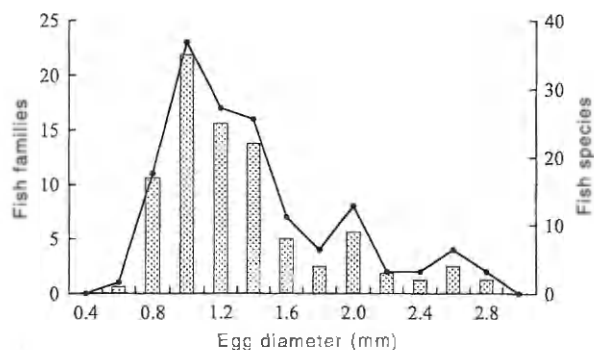


Fig. 1. Size-frequency distribution of egg diameters in (■) 139 marine fish species, also grouped into (●) 103 families (based on data in FishBase98, see Froese & Pauly 1998). A log-normal distribution centered around 1.0 mm is observed.

Relationships between growth and respiration

While local conditions (food, temperature etc.) do affect the precise course of the growth of fish and the timing of their maturation, clear patterns emerge when for different populations and species, K (expressing the rate at which the asymptote of the von Bertalanffy growth curves is approached) is plotted against the corresponding asymptotic size, expressed either in length (L_{∞}) or weight (W_{∞}). Figure 3 shows such patterns for fish in general, based on groups as diverse as gobies ($L_{\infty} =$

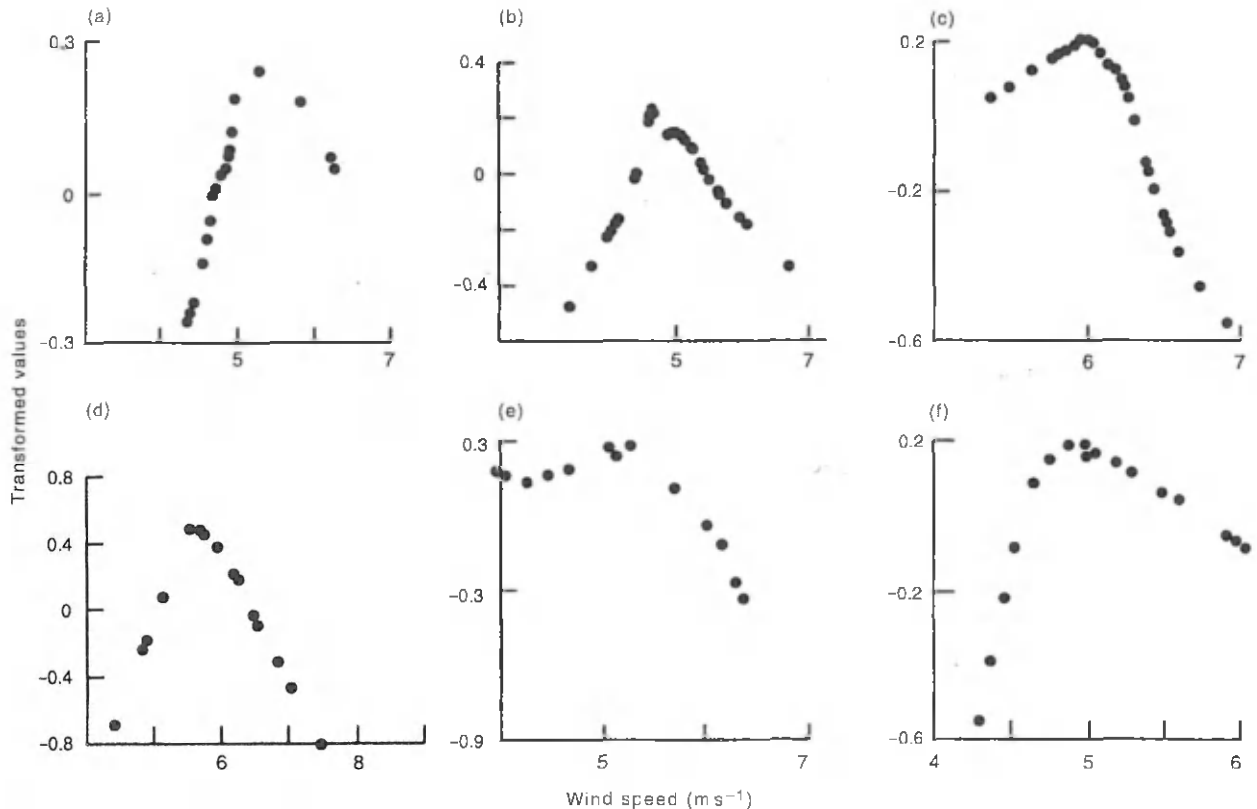


Fig. 2. Dome-shaped pattern between pelagic fish recruitment and wind-speed in different upwelling areas and for different species, as obtained by the alternating conditional expectation algorithm. The transformed value (Y-axis) indicates the shape of the transformation that is suitable for the X-values. The pattern obtained defines the optimal environmental window and explains approximately 20% of the recruitment variance (adapted from Cury & Roy 1989, Cury *et al.* 1995, Serra *et al.* 1998). (a), Californian sardine; (b), Californian anchovy; (c), Peruvian anchoveta; (d), Chilean sardine; (e), Moroccan sardine; (f), Senegalese sardinella.

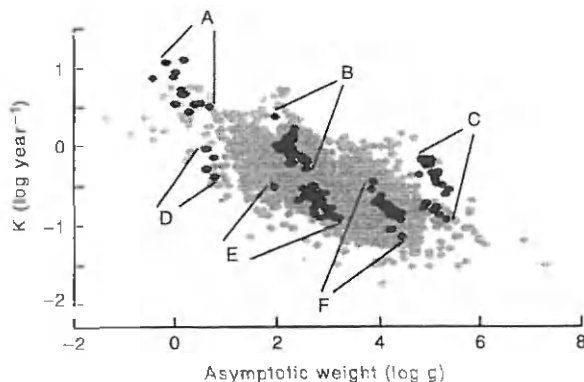


Fig. 3. Plot of the parameter K of the von Bertalanffy growth function against the corresponding estimate of asymptotic weight in 2948 different populations of 608 species of fishes, of which six are highlighted (Based on data in FishBase98, see Froese & Pauly 1998). A, *Spratellodites delicatulus*; B, *Decapterus macrosoma*; C, *Thunnus albacarar*; D, *Cottus gobio*; E, *Trachurus trachurus*; F, *Scomberomorus cavalla*.

1.2 cm), whale sharks ($L_{\infty} = 16$ m), fast-growing tunas, slow-growing rockfishes, etc.

On auximetric ('growth measuring') plots such as Fig. 3, the different stocks of individual species form distinct ellipsoid clusters, whose main axis has, an average slope of -2 (when $\log K$ is plotted against $\log L_{\infty}$) or $-2/3$ (when $\log K$ is plotted against $\log W_{\infty}$), which is much steeper than the slope of the cluster representing fishes as a whole (Fig. 3). Genera form larger clusters, with slopes that are less steep, and this is even more marked when families are plotted, whose average slope often approximates that of the pattern for all fishes (Fig. 3). Such propensities cannot be explained by local conditions (i.e. fish stock X in the Bay of Y in year Z had a certain set of growth parameters 'because' of El Niño effects in that year), although this is still commonly seen in the literature.

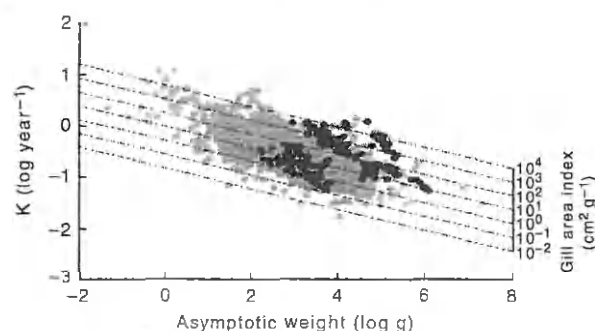


Fig. 4. Plot of the parameter K of the von Bertalanffy growth function against the corresponding estimate of asymptotic weight (W_{∞}) in 2948 fish populations (608 species), with superimposed isolines predicting K , given W_{∞} and Gill Area Index (GI; in $\text{cm}^2 \text{g}^{-1}$) values. The isolines are derived from a multiple regression, including 52 species, of $\log K$ against $\log W_{\infty}$ and gill area at $\log W_{\infty}$, the latter estimated from $\text{GI} \times \log W_{\infty}^{0.8}$; details in FishBase (Froese & Pauly 1998; Pauly 1998a). This plot suggests that fish of a given size can exhibit rapid growth (high K values) only if they have large gills, as illustrated here by the contrast between the fast-growing Thunninae (●, tunas and frigate mackerels) and the slower-growing Pleuronectidae (⊙, flatfishes).

Rather, local conditions can only modify pre-existing propensities, themselves due to some conserved features of the species in question.

Given the properties of water, particularly with regard to dissolved O_2 (see above), a theory has been proposed which suggests that it is O_2 supply through the gills, and hence gill area itself, which acts as the limiting factor for fish growth (Pauly 1979, 1981, 1997, 1998a, 1998b). While we cannot discuss the various corollaries of this theory here, we present a new graph illustrating its key feature: the relationship between the gill area of fishes and their position on an auximetric grid (Fig. 4).

Relationships between natural mortality and growth

Individual growth, in fishes, must compensate for the huge loss of eggs and larvae alluded to above, and growth parameters can thus be expected to be closely related to natural mortality (M). This is illustrated here in Fig. 5, using what is probably the largest set of independent estimates of M available for any group of animals. As expected, M

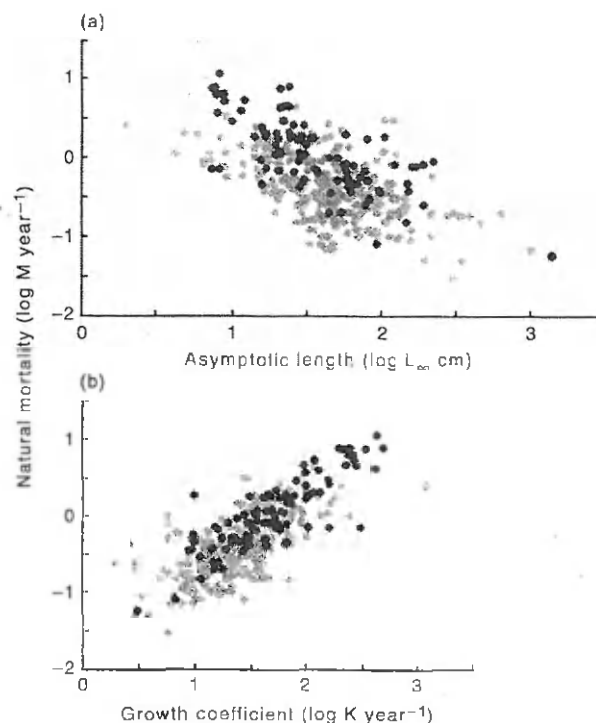


Fig. 5. Relationship between natural mortality (M) and growth parameters in 358 fish populations, representing 215 species (based on data in FishBase98, see Froese & Pauly 1998). (a), Plot of M against asymptotic length (L_{∞}); (b), Plot of M against the parameter K of the von Bertalanffy growth function. Note the propensity for M to be higher in (●) warm-water ($>20^{\circ}\text{C}$; $n=105$) than in (⊙) cold-water populations, given values of L_{∞} (a) and/or K (b).

correlates strongly with the growth parameters L_{∞} and K , thus confirming earlier analyses based on smaller data sets (Pauly 1980). Moreover, the plots also document a strong temperature impact on M ; this effect is quite understandable if temperature is assumed to affect life history via respiration and growth. However, the strong effect of temperature on M is problematic for theories in which the ratio M/K is supposed to be 'invariant' (Charnov 1993).

DISCUSSION

Fish have been very successful on earth, and in fact they comprise more than half of all described vertebrates. This success is linked to the particular life history traits that evolved to ensure survival in a viscous, turbulent and nutritionally dilute environment. We view the two sets of propensities

concerning reproduction and growth illustrated above, as important elements of any theory that strives to explain the dynamics of marine fishes. An extension of the fundamental mechanisms we present here may explain why populations tend to maintain themselves over time. This, we propose, would be a useful counterpoint to the present emphasis on population 'variability', a phenomenon far less wondrous, if one stops to think about it, than population constancy in the face of environmental variability (Ursin 1973; Cury 1994; Le Page & Cury 1997). Such a shift of emphasis would also acknowledge the fundamental differences, illustrated here, between marine and terrestrial environments. In particular, marine fishes have been shaped by strong constraints, which once overcome, have produced strongly convergent features, and thence predictable patterns. Extracting patterns and propensities in nature could be much more tractable in marine ecology than in terrestrial ecology.

ACKNOWLEDGEMENTS

The authors would like to thank Dr Claude Roy for comments and Alasdair Beattie and Aque Atanacio for preparing the figures.

REFERENCES

- BAKUN A. (1996) *Patterns in the Ocean: Ocean Processes and Marine Population Dynamics*. California Sea Grant College System, University of California, La Jolla.
- BASCOMPTE J. & SOLÉ R. V. (1998) Spatiotemporal patterns in nature. *Trends in Ecology and Evolution* 13: 173–174.
- CHAMBERS R. C. (1997) Environmental influences on egg and propagule sizes in marine fishes. In: *Early Life History and Recruitment in Fish Populations* (eds R. C. Chambers & E. A. Trippel) pp. 63–102. Chapman & Hall, London.
- CHARNOV E. (1993) *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology*. Oxford University Press, Oxford.
- CURY P. (1994) Obstinate nature: An ecology of individuals: Thoughts on reproductive behavior and biodiversity. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 1664–1673.
- CURY P. & ROY C. (1989) Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 670–680.
- CURY P., ROY C., MENDELSSOHN R., BAKUN A., HUSBY D. M. & PARRISH R. H. (1995) Moderate is better: Exploring nonlinear climatic effect on Californian anchovy (*Engraulis mordax*). *Canadian Journal of Fisheries and Aquatic Sciences* 127: 417–424.
- CUSHING D. H. (1996) Towards a science of recruitment in fish populations. In: *Excellence in Ecology 7* (ed. O. Kinne) Ecology Institute, Oldendorf/Luhe, Germany.
- FROESE R. & PAULY D. (eds) (1998) *FishBase 98: Concepts, Design and Data Sources*. International Centre for Living Aquatic Resources Management, Manila.
- KULLENBERG G. (1978) Vertical processes and the vertical–horizontal coupling. In: *Spatial Pattern in Plankton Communities* (ed. J. H. Steele) pp. 43–71. Plenum Press, New York.
- LE PAGE C. & CURY P. (1997) Population viability and spatial fish reproductive strategies in constant and changing environments: An individual-based modelling approach. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 2235–2246.
- LEVIN S. A. (1993) Approaches to forecasting biomass yields in large marine ecosystems. In: *Large Marine Ecosystems: Stress, Mitigation and Sustainability* (eds K. Sherman, L. M. Alexander & B. D. Gold) pp. 36–39. American Association for the Advancement of Science, Washington.
- PAULY D. (1979) Gill size and temperature as governing factors in fish growth: A generalization of von Bertalanffy's growth formula. *Berichte des Institut für Meereskunde an der Universität Kiel* 63: 156.
- PAULY D. (1980) On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. *Journal du Conseil International pour l'Exploration de la Mer* 39: 175–192.
- PAULY D. (1981) The relationships between gill surface area and growth performance in fish: A generalization of von Bertalanffy's theory of growth. *Meeresforschung* 28: 251–282.
- PAULY D. (1997) Geometrical constraints on body size. *Trends in Ecology and Evolution* 12: 442–443.
- PAULY D. (1998a) Tropical fishes: Patterns and propensities. *Journal of Fish Biology* 53 (Supplement A): 1–17.
- PAULY D. (1998b) Why squids, though not fish, may be better understood by pretending they are. *South African Journal of Marine Science* 20: 47–58.

- PETERS R. H. (1992) *A Critique for Ecology* (2nd edn). Cambridge University Press, Cambridge.
- POPPER K. (1996) *A World of Propensities*. Thoemmes, Bristol.
- SERRA R., CURY P. & ROY C. (1998) The recruitment of the Chilean sardine (*Sardinops sagax*) and the 'optimal' environmental window'. In: *From Local to Global Changes in Upwelling Systems* (eds M. H. Durand, P. Cury, R. Mendelsohn, C. Roy, A. Bakun & D. Pauly) pp. 267-274. Editions de l'Institut de Recherche pour le Développement, Paris.
- SHIN Y., ROY C. & CURY P. (1998) Reproductive strategies of pelagics in upwelling areas: A generalization. In: *From Local to Global Changes in Upwelling Systems* (eds M. H. Durand, P. Cury, R. Mendelsohn, C. Roy, A. Bakun & D. Pauly) pp. 409-422. Editions de l'Institut de Recherche pour le Développement, Paris.
- STEELE J. H. (1985) A comparison of terrestrial and marine ecological systems. *Nature* 313: 355-358.
- STEELE J. H. (1995) Can ecological concepts span the land and ocean domains? In: *Ecological Time Series* (eds T. M. Powell & J. H. Steele) pp. 5-19. Chapman & Hall, New York.
- TERRIAULT J. C. & PLATT T. (1981) Environmental control of phytoplankton patchiness. *Journal of Fisheries Research Board of Canada* 38: 368-641.
- URSIN E. (1973) Stability and variability in the marine ecosystem. *Dana* 2: 51-67.