# LIFE HISTORIES PREDICT VULNERABILITY TO FISHERIES EXPLOITATION

**Simon Jennings[a,b], John Reynolds[b], Simon Greenstreet[c] & Nicholas Polunin[d]**

[a] CEFAS, Lowestoft Laboratory, [b] University of East Anglia, Norwich [c] Marine Laboratory, Aberdeen, & [d] University of Newcastle upon Tyne, UK

*Knowledge of life histories may help to predict the vulnerability of these snappers to exploitation*

***Fisheries exploitation has led to decreases in the abundance of many target and non-target species while others have increased in abundance despite intensive fishing [6,9].***

***For conservation and management purposes we need to know the characteristics of exploited species that make them vulnerable to fishing. In this poster we show how fish life histories and phylogenetic relationships can be used to:***

- ***understand structural change in exploited communities***
- ***identify life history correlates of responses to exploitation***
- ***predict relative vulnerability of populations to exploitation***

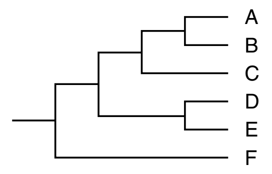
*Slow growing sharks can sustain lower levels of fishing mortality than species with 'faster' life histories*

## Background

Theoretical analyses suggest that large, slow-growing and late-maturing species exhibit greater rates of population decline for given rates of fishing mortality than species with 'faster' life histories[1,13,15]. Empirical tests of these theories are more difficult because related taxa have evolved together and cannot be treated as independent data points in analyses that link life histories and population trends (Box 1). For example, many skate and ray species have decreased in abudance following fishing, a response which has been attributed to their advanced ages at maturity and low fecundity. However, because they evolved together, members of this genus share many other characteristics such as broad body shape and laying demersal egg cases which could also account for their susceptibility to fishing. Only a comparison between members of this genus, or between stocks of one species, would eliminate these other variables they have in common[7]. In our analyses we have used phylogenetic comparative approaches[5,7] to eliminate spurious correlations among the life histories of related taxa and derive life history and abundance parameters that are statistically independent (Box 2).

### Box 1 *Related taxa share characteristics because they evolved together.*

Consider this simple phylogeny for six species A-F.



Species A and B are more likely to share characteristics than A and F or B and F because A and B are more closely related. Thus the life history parameters of A, B and F cannot be treated as independent data points in an analysis.

### Box 2 *Calculation of contrasts*

To account for phylogenetic relationships between taxa and to yield data that are phylogenetically and statistically independent, contrasts are calculated. Contrasts are the differences in parameters between closely related species. Each contrast yields one independent data point to be entered into the analysis.

Contrasts in life history parameters are usually set to positive. This is done by subtracting the parameter of lower value from the parameter of higher value. For example, to calculate a contrast in maximum length ($L_{max}$) for the related grouper species *Cephalopholis argus* and *Cephalophlos urodeta,* the $L_{max}$ for *C. urodeta* is subtracted from $L_{max}$ for *C. argus*. To relate contrasts in life history parameters to contrasts in abundance trends, contrasts in abundance trends are calculated for the same species pairs in the same sequence. Thus contrasts in abundance trends may be positive or negative.

| Species | $L_{max}$ | Contrast in $L_{max}$ | Trend | Contrast in trend |
|---|---|---|---|---|
| *Cephalopholis argus* | 40 | 13 | -0.00278 | -0.00074 |
| *Cephalopholis urodeta* | 27 | | -0.00204 | |

To determine which contrasts should be made, it is necessary to construct a phylogeny showing the evolutionary relatedness between species. Such phylogenies are shown in Figures 2 and 4.

## Structural change in exploited communities

An understanding of the links between life histories and responses to exploitation could provide the basis for predicting shifts in community structure by identifying susceptible species and linking life history tactics with population dynamics. We examined long-term trends in the abundance of species in the North Sea bottom-dwelling (demersal) fish community.

Between 1925 and 1996, changes in species composition led to an increase in mean growth rate while mean maximum size, age at maturity and size at maturity decreased (Figure 1). The demersal fish community was increasingly heavily fished during this period[6].

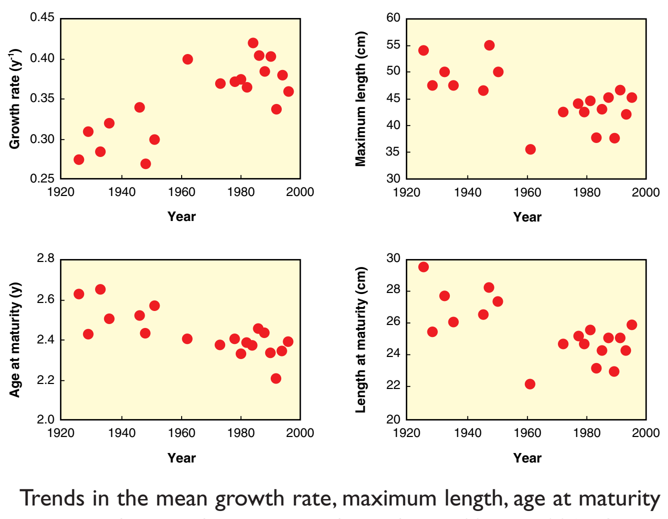
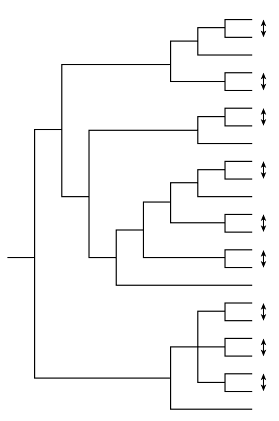


*Figure 1* Trends in the mean growth rate, maximum length, age at maturity and length at maturity of North Sea demersal fishes from 1925 to 1996. Growth rate and maximum length were described using the parameters K and $L_\infty$ of the von Bertalanffy growth equation. Age and length at maturity were the mean age (years) or length (cm) at which 50% of the stock attained maturity.

Trends in mean life history characteristics of the community were linked to trends in abundance of component species (Figure 2). In eight of the nine pairs of taxa, the species that declined in abundance relative to its nearest relative had a larger body size (Binomial Test, $P = 0.020$). These species were also slower growing ($P = 0.020$). Similarly, contrasts in age and size at maturity indicated that species that decreased in abundance with respect to their closest relatives were larger and older at maturity ($P = 0.035$) (Figure 3). The phylogenetically-based analyses demonstrated that trends in community structure could be explained from the differential responses of related species to fishing[10].



| Species | Common Name | Abundance trend[1] | Life history parameters[2] | | | |
|---|---|---|---|---|---|---|
| | | | $L_\infty$ | K | $T_m$ | $L_m$ |
| *Raja naevus* | cuckoo ray | -0.027 | 92 | 0.11 | 9.0 | 59 |
| *Raja radiata* | starry ray | +0.013 | 66 | 0.23 | 4.0 | 4 |
| *Raja batis* | common skate | -0.030 | 254 | 0.06 | 11.0 | 130 |
| *Squalus acanthias* | spurdog | -0.051 | 90 | 0.15 | 6.5 | 67 |
| *Scyliorhinus canicula* | lesser spotted dogfish | +0.002 | 88 | 0.20 | 5.0 | 58 |
| *Eutrigla gurnardus* | grey gurnard | -0.015 | 46 | 0.16 | 3.0 | 23 |
| *Sebastes viviparus* | Norway haddock | -0.005 | 36 | 0.07 | - | - |
| *Callionymus lyra* | dragonet | -0.024 | 23 | 0.47 | 2.5 | 13 |
| *Melanogrammus aeglefinus* | haddock | +0.004 | 68 | 0.19 | 2.5 | 34 |
| *Merlangius merlangus* | whiting | +0.005 | 42 | 0.32 | 1.5 | 20 |
| *Gadus morhua* | cod | +0.007 | 123 | 0.23 | 3.8 | 70 |
| *Trisopterus minutus* | poor cod | -0.007 | 20 | 0.51 | 2.0 | 15 |
| *Trisopterus esmarkii* | Norway pout | +0.012 | 23 | 0.52 | 2.3 | 19 |
| *Brosme brosme* | torsk | -0.000 | 89 | 0.08 | 7.0 | 50 |
| *Enchelyopus cimbrius* | four-bearded rockling | +0.009 | 36 | 0.20 | 3.0 | 25 |
| *Lophius piscatorius* | anglerfish | -0.015 | 106 | 0.18 | 4.5 | 61 |
| *Glyptocephalus cynoglossus* | witch | -0.020 | 44 | 0.20 | 4.5 | 29 |
| *Microstomus kitt* | lemon sole | -0.003 | 37 | 0.42 | 4.0 | 27 |
| *Pleuronectes platessa* | plaice | -0.005 | 54 | 0.11 | 2.5 | 27 |
| *Limanda limanda* | dab | +0.005 | 27 | 0.26 | 2.3 | 13 |
| *Hippoglossus hippoglossus* | halibut | -0.015 | 204 | 0.10 | 5.8 | 83 |
| *Hippoglossoides platessoides* | long rough dab | -0.005 | 25 | 0.34 | 2.6 | 15 |
| *Lepidorhombus whiffiagonis* | megrim | -0.022 | 54 | 0.12 | 3.0 | 23 |

*Figure 2* Phylogenetic relationships, abundance trends and life history parameters for species in the North Sea fish community. The species listed accounted for 99% of all individuals caught during scientific trawl surveys in the northern North Sea from 1925 to 1996. Arrows indicate the pairs of species for which contrasts were calculated. For each pair of species we subtracted the value of the life history trait for the species that had increased in relative abundance from the value of the trait for the species that decreased in relative abundance.

[1] Abundance trend: slope of linear relationship between standardised catch rate (numbers $h^{-1}$) in the Scottish groundfish survey and time (years).

[2] Life history parameters: follow Figure 1.

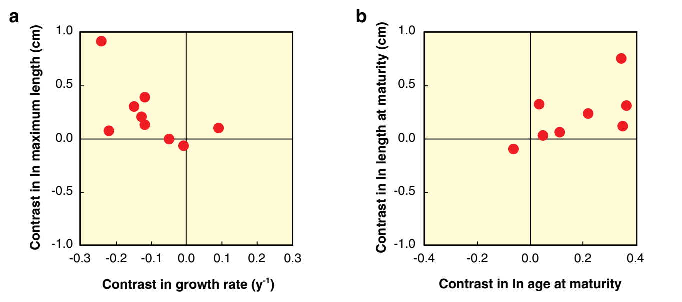


*Figure 3* Differences in (a) the maximum length and growth rate and (b) the age and length at maturity between pairs of related species that exhibited opposing population trends.

## Life history correlates of responses to exploitation

We used an approach based on phylogenetic comparisons to identify life history correlates of abundance trends in 18 intensively exploited fish stocks from the northeast Atlantic. Changes in abundance were expressed as the slope of the relationship between ln abundance and time for the period 1975 to 1994. We accounted for differences in fishing mortality by taking the residuals from the relationship between contrast in abundance change and contrast in mean fishing mortality. The comparative analysis showed that those fishes that decreased in abundance compared with their nearest relatives matured later, attained larger maximum size, and exhibited significantly lower potential rates of population increase[11].

## Relative vulnerability of populations to exploitation

Fishing has led to local extirpations of tropical reef fishes. For conservation purposes it is important to identify all those species that are vulnerable to fishing but this cannot be done using *a-priori* assessments or by describing trends in abundance because the necessary scientific resources are not available. Thus the predictions of vulnerability which provide the basis for conservation action will have to be made using existing data or data that can be acquired rapidly before further extirpations occur.

The two studies described above have shown that life histories determine the response of a species to exploitation. Although parameters such as growth rates and age at maturity are not known for many reef species the classic studies of Beverton and others have demonstrated that they are closely related to other life history parameters[2, 3, 4, 14]. Thus it may be possible to use an easily measured parameter, such as maximum size, as a surrogate for parameters that cannot be measured.

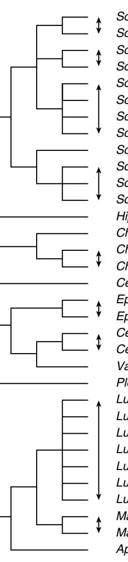
We used a phylogenetic comparative approach to demonstrate that species of grouper (Epinephelinae), snapper (Lutjanidae) and parrotfish (Scaridae) that decreased in abundance more than their nearest phylogenetic relative had greater maximum size (Figures 4 and 5). Our results suggest that it may be possible to predict the vulnerability of reef fishes to exploitation based on responses of their relatives. The quality of prediction was good for the intensively fished groupers and snappers but poor for the lightly fished parrotfishes.

## Acknowledgements

***We thank the EC, NERC and DIFD, UK for funding.***

**The Centre for Environment, Fisheries and Aquaculture Science,
Lowestoft, NR33 OHT, United Kingdom.**

**Email: S. Jennings@cefas.co.uk.**



| Species | Common Name | Abundance trend[1] | Maximum length (cm) [2] |
|---|---|---|---|
| *Scarus frenatus* | bridled parrotfish | -0.00200 | 47 |
| *Scarus niger* | swarthy parrotfish | +0.00048 | 35 |
| *Scarus dimidiatus* | swarthy parrotfish | -0.00093 | 31 |
| *Scarus oviceps* | egghead parrotfish | -0.00045 | 32 |
| *Scarus altipinnis* | minifin parrotfish | -0.00128 | 60 |
| *Scarus globiceps* | globehead parrotfish | +0.00079 | 30 |
| *Scarus rubroviolaceus* | ember parrotfish | -0.00070 | 70 |
| *Scarus spinus* | greensnout parrotfish | -0.00001 | 32 |
| *Scarus forsteni* | whitespot parrotfish | +0.00006 | 55 |
| *Scarus chameleon* | chameleon parrotfish | +0.00006 | 31 |
| *Scarus psittacus* | palenose parrotfish | +0.00031 | 30 |
| *Scarus schlegeli* | Schlegel's parrotfish | +0.00231 | 38 |
| *Hipposcarus longiceps* | longnose parrotfish | -0.00202 | 44 |
| *Chlorurus gibbus* | steephead parrotfish | -0.00148 | 70 |
| *Chlorurus bleekeri* | Bleeker's parrotfish | -0.00045 | 33 |
| *Chlorurus sordidus* | bullethead parrotfish | -0.00024 | 40 |
| *Cetoscarus bicolor* | bicolour parrotfish | -0.00204 | 80 |
| *Epinephelus merra* | dwarf spotted grouper | +0.00018 | 28 |
| *Epinephelus polyphekadion* | camouflage grouper | -0.00300 | 61 |
| *Cephalopholis argus* | peacock grouper | -0.00278 | 40 |
| *Cephalopholis urodeta* | darkfin hind | -0.00204 | 27 |
| *Variola louti* | coronation grouper | -0.00004 | 100 |
| *Plectropomus laevis* | blacksaddle coral trout | -0.00273 | 100 |
| *Lutjanus bohar* | red bass | -0.00424 | 100 |
| *Lutjanus fulviflamma* | dory snapper | -0.00250 | 35 |
| *Lutjanus fulvus* | blacktail snapper | -0.00039 | 40 |
| *Lutjanus gibbus* | humpback snapper | -0.00322 | 50 |
| *Lutjanus kasmira* | bluestriped snapper | -0.00269 | 35 |
| *Lutjanus monostigma* | onespot snapper | -0.00120 | 50 |
| *Lutjanus semicinctus* | blackbanded snapper | -0.00009 | 35 |
| *Macolor macularis* | midnight snapper | -0.00180 | 55 |
| *Macolor niger* | black and white snapper | +0.00036 | 55 |
| *Aphareus furca* | smalltoothed jobfish | -0.00032 | 40 |

*Figure 4* Phylogenetic relationships, abundance trends and maximum size for species in the Fijian reef fish community

[1] Abundance trend is the slope of the relationship between ln (biomass g $m^{-2}$ +1) and fishing intensity (fishers km reef $front^{-1}$).

[2] Maximum length is the maximum observed length of the species at any location. Arrows indicate pairs or groups for which contrasts were calculated. In the three cases where phylogenetic relationships between species could not be resolved we calculated all $(n^2-n)/2$ contrasts for each group and presented mean values.

Two factors will determine the response of a population to exploitation: the fishing mortality rate and the potential rate of population increase. Larger species can sustain lower fishing mortality rates than smaller species but may also suffer higher fishing mortality because they are more desirable targets for fishers. Given the logistical difficulties and expense associated with collecting basic population and fishery data, reliable estimates of fishing mortality cannot be made for most species caught on tropical reefs. As such, and in contrast with our studies of north-east Atlantic stocks, we will never know the relative roles of fishing mortality and life histories in the response to exploration. Nevertheless, our approach may help proactive conservationists and fishery managers identify and conserve vulnerable species in new, developing or lightly exploited fisheries, thereby reducing their reliance on reactive management methods[12].

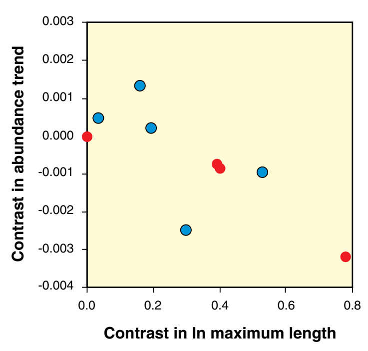


*Figure 5* Relationships between contrasts in trends in abundance (measured as biomass) and contrasts in maximum size for Fijian reef fishes. Blue circles represent parrotfishes, red circles represent groupers and snappers. The relationship between the contrast in abundance trend and contrast in maximum size is significant ($F_{1,8}$= 12.02, $p$= 0.008). The analysis shows that, after accounting for phylogenetic relationships between species, species of greater maximum size are more vulnerable to fishing.

## References

1. Beddington, J. R. & Cooke, J. G. (1983) The potential yield of fish stocks. *FAO Fisheries Technical Paper,* 242.
2. Beverton, R. J. H. & Holt, S. J. (1959) A review of the lifespan and mortality rates of fish in nature and their relationship to growth and other physiological characteristics. *Ciba Foundation Colloquim on Ageing,* 5, 1 42-180.
3. Beverton, R. J. H. (1963) Maturation, growth and mortality of Clupeid and Engraulid stocks in relation to fishing. *Rapports et ProcÈs-Verbaux des RÈunions, Conseil International pour l'Exploration de la Mer,* 154, 44-67.
4. Charnov, E. L. (1993) Life history invariants: some explorations of symmetry in evolutionary ecology Oxford University Press, Oxford.
5. Felsenstein, J. (1985) Phylogenies and the comparative method. *American Naturalist,* 125, 1-15.
6. Greenstreet, S. P. R. & Hall, S. J. (1996) Fishing and ground-fish assemblage structure in the north-western North Sea: an analysis of long-term and spatial trends. *Journal of Animal Ecology,* 65, 577-598.
7. Harvey, P. H. & Pagel, M. D. (1991) The comparative method in evolutionary biology Oxford University Press, Oxford.
8. Jennings, S. & Polunin, N.V. C. (1997) Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. *Coral Reefs,* 16, 71-82.
9. Jennings, S. & Kaiser, M. J. (1998) The effects of fishing on marine ecosystems. *Advances in Marine Biology,* 34, 201-352.
10. Jennings, S., Greenstreet, S. P. R. & Reynolds, J. D. (1999) Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology,* 68, 617-627.
11. Jennings, S., Reynolds, J. D. & Mills, S. C. (1998) Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society: Biological Sciences,* 265, 333-339.
12. Jennings, S., Reynolds, J. D. & Polunin, N.V. C. (1999) Predicting the vulnerability of tropical reef fishes to exploitation using phylogenies and life histories. *Conservation Biology,* 13, 1466-1475.
13. Kirkwood, G. P., Beddington, J. R. & Rossouw, J. A. (1994) Harvesting species of different lifespans. In: *Large-scale ecology and conservation biology,* (ed P. J. Edwards, R. M. May & N. R. Webb), pp. 199-227. Blackwell Scientific, Oxford.
14. Pauly, D. (1980) On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. *Journal du Conseil, Conseil International pour l'Exploration de la Mer,* 39, 175-192.
15. Trippel, E. A. (1995) Age at maturity as a stress indicator in fishes. *BioScience,* 45, 759-771.