

LIFE HISTORY PATTERNS IN MARINE FISHES AND THEIR CONSEQUENCES FOR FISHERIES MANAGEMENT

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ABSTRACT

Natural selection operates at the life history level to maximize the number of surviving offspring. Life history characteristics will vary in consistent patterns to meet this constraint. When theoretical patterns in life histories were investigated in terms of r and K selection and compared with actual trends in life history characteristics of fishes, the agreement between observed and predicted trends was significant. The effects of harvesting on stocks with these life history trends were investigated and it was found that K selected type species would be highly sensitive to overfishing and, once depleted, recovery would require a long time.

The ecological and genetic properties of a species are intimately linked. The morphological and reproductive characteristics, population sizes, and genetic frequencies of species are adjusted to their environments by natural selection. Species inhabiting different environments show different patterns of life history characteristics. The relationship among habitat, ecological strategies, and population parameters has been termed r and K selection (MacArthur and Wilson 1967) and/or optimal life histories (Gadgil and Bossert 1970). This body of theory is based on the assumption that natural selection operates on these characteristics in order to maximize the number of surviving offspring produced. Under an environmental regime with a large component of unpredictable, nonselective, mortality an organism will allocate a larger portion of its resources to reproductive activities (an r strategist). Conversely the optimal allocation of resources for a population subjected to a high proportion of predictable, selective mortality will be toward increasing individual fitness, frequently through competitive ability (a K strategist). With the number and variability of factors operating on any particular species, no species is going to be an r or K strategist in an absolute sense. A species will only occupy a relative position on the r and K continuum.

In fisheries biology, the value of comparative studies of life history parameters has long been recognized (Holt 1962; Beverton 1963; Cushing 1971; Alverson and Carney 1975). These life his-

tory parameters should vary in a consistent pattern which can be predicted from the theory of r and K selection. In this paper, these predictions are tested with life history parameters from major groups of marine fishes. The theory has implications for management, particularly when fisheries are in the initial stages of development.

THEORY OF r AND K SELECTION

The theory of r and K selection is based on two assumptions about the allocation of a population's resources between competitive and reproductive functions (Pianka 1974; Gadgil and Bossert 1970; Schaffer and Gadgil 1975). The first is that there is a positive relationship between the amount of resources spent on an offspring and the fitness of that offspring. The second assumption is that any species only has a fixed amount of resources available. This results in an inverse relationship between the number of offspring produced and their average fitness. The criterion for success in natural selection is the number of surviving offspring that a parent produces (Crow and Kimura 1970). Therefore, the best reproductive strategy is a compromise between two conflicting demands: production of the largest possible total number of offspring (r selection), and production of offspring with the highest possible fitness (K selection). The particular point of compromise for any species will be a function of the selection factors operating on that species and would be that species' position on the r and K continuum.

The second part of the theory concerns the relationship between these life history strategies and

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the habitat the species occupies (Southwood et al. 1974; Southwood and Comins 1976). If mortality factors in an environment are variable and/or unpredictable, then their effects are likely to be less selective in terms of population size or of the phenotype involved. Under these circumstances, individual competitive fitness is of relatively less importance. The best strategy would be to place maximal resources into reproduction and produce as many offspring as possible (r selection).

The contrasting situation is an environment in which mortality factors are stable and/or predictable. Mortality under these circumstances will result in strong selection for individual fitness and there will be pronounced differences between their effects on different phenotypes. In these stable environments, the optimal strategy would be to produce offspring with substantial competitive ability (K selection). Due to the previously assumed relationship between fitness per offspring and the number of offspring produced, this also means the production of fewer offspring.

The two situations described above are end points of a spectrum. Species will always have a number of different selective pressures operating on them, both spatially and temporally. This is particularly evident in aquatic organisms which characteristically go through several life history stages. This again emphasizes that the concept of r and K selection should be applied only in a comparative sense. Finally, comparisons must be made between species of a similar ecological nature. Comparisons between species of different ecological types is meaningless since fundamentally different types of selective factors will be operating in those cases.

r AND K SELECTION IN MARINE FISHES

Natural selection will favor nonreproductive activities at the expense of reproductive activities only when they enhance reproduction at later stages in the life history and thereby maximize overall survival (Crow and Kimura 1970). Changes in allocation of a species' resources from reproductive to competitive activities will only occur in habitats where competitive activities enhance the survival of future offspring. The result of this is that organisms under different selection pressures will have characteristic life history patterns. An r selected species will have life history strategies which tend toward productivity. The K

selected species will have life strategies which tend toward efficient exploitation of a specific limiting resource (Pianka 1974). Therefore, specific combinations of population parameters can be identified as being characteristic of an r strategist, while the opposing combination would be characteristic of a K strategist.

A species which is exposed to a large component of nonselective or catastrophic mortality (i.e., an r strategist) would be selected for characteristics that would increase productivity. Increasing productivity through reproductive activity generally implies: 1) early maturity, 2) rapid growth rates, 3) production of larger numbers of offspring at a given parental size, and 4) maximum production of offspring at early age (Gadgil and Bossert 1970). Other characteristics which are results of the allocation of large portions of resources to reproductive activity are: 1) small body size, 2) high rates of mortality, and 3) shorter life span (Pianka 1974; Gadgil and Solbrig 1972). In terms of commonly measured population parameters in fishery biology, an r selected species would have: 1) a low age at first maturity, 2) a high value of k from the von Bertalanffy growth equation, 3) a small L_{∞} from the von Bertalanffy growth equation, 4) high rates of instantaneous natural mortality (M), and 5) low maximum age.

Even in environments with predictable mortality sources, increased allocation of resources to competitive activities will only occur when two prerequisites are met (Schaffer and Gadgil 1975). The first is that reproductive potential increases with some function of age. The second is that there is some additional mortality risk associated with reproduction. Under these assumptions, the attributes associated with a K strategist would be: 1) delayed maturity, 2) reduced growth rates, 3) low mortality rates, 4) large body size, and 5) longer life span. Again in terms measured in fishery biology, a K selected species would have: 1) a high age at first maturity, 2) a low k from the von Bertalanffy growth equation, 3) a large L_{∞} from the von Bertalanffy growth equation, 4) low M , and 5) a high maximum age.

Using these life history correlates of r and K selection (summarized in Table 1), it is possible to predict the signs of a correlation matrix between life history parameters (Table 2). The predicted matrix can be compared with actual matrices calculated using Spearman's rank correlation coefficient. This coefficient only assumes that the observed data are mutually independent and come

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TABLE 1.—Summary of hypothetical *r* and *K* correlates in life history parameters of fishes.

Characteristics	<i>r</i> selected	<i>K</i> selected
Body size, L_{∞}^1	Small	Large
Maximum age	Low	High
Age at first maturity	Low	High
Natural mortality, <i>M</i>	High	Low
Growth rate, k^1	High	Low

¹The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 2.—Predicted signs of correlation matrix of life history parameters in fishes.

Characteristics	L_{∞}^1	Maximum age	Age at first maturity	<i>M</i>	k^1
Body size, L_{∞}^1	1.0	+	+	-	-
Maximum age		1.0	+	-	-
Age at first maturity			1.0	-	-
Natural mortality, <i>M</i>				1.0	+
Growth rate, k^1					1.0

¹The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

from a continuous bivariate population (Hollander and Wolfe 1973).

RESULTS

Life history parameters were gathered from the literature for several major groups of marine fishes. Often there were multiple sets of data for the same species from different locations. Each set of values was used as a separate data case. The literature citations for the actual parameters are listed by group in Appendix I. Correlation matrices were calculated for the following groups of fish: 1) herring and anchovies, Clupeidae and Engraulidae (Table 3), 2) salmon, Salmonidae (Table 4), 3) cods, Gadidae (Table 5), 4) rockfishes,

TABLE 3.—Correlation coefficients between life-history parameters for herring and anchovies (families Clupeidae and Engraulidae). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_{∞}^1	Maximum age	Age at first maturity	<i>M</i>	k^1
Body size, L_{∞}^1	1.0	0.846 (0.001)	0.816 (0.001)	-0.746 (0.001)	-0.720 (0.001)
Maximum age		1.0	0.904 (0.001)	-0.797 (0.001)	-0.763 (0.001)
Age at first maturity			1.0	-0.702 (0.001)	-0.732 (0.001)
Natural mortality, <i>M</i>				1.0	0.876 (0.001)
Growth rate, k^1					1.0

¹The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 4.—Correlation matrix between life-history parameters for salmon (family Salmonidae). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_{∞}^1	Maximum age	Age at first maturity	<i>M</i>	k^1
Body size, L_{∞}^1	1.0	0.765 (0.001)	0.728 (0.032)	-0.785 (0.001)	-0.730 (0.002)
Maximum age		1.0	0.776 (0.020)	-0.737 (0.003)	-0.674 (0.004)
Age at first maturity			1.0	-0.644 (0.084)	-0.812 (0.013)
Natural mortality, <i>M</i>				1.0	0.896 (0.001)
Growth rate, k^1					1.0

¹The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 5.—Correlation matrix between life-history parameters for cods (family Gadidae). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_{∞}^1	Maximum age	Age at first maturity	<i>M</i>	k^1
Body size, L_{∞}^1	1.0	0.795 (0.002)	0.833 (0.001)	-0.647 (0.022)	-0.666 (0.001)
Maximum age		1.0	0.737 (0.014)	-0.654 (0.028)	-0.702 (0.008)
Age at first maturity			1.0	-0.715 (0.035)	-0.658 (0.008)
Natural mortality, <i>M</i>				1.0	0.950 (0.001)
Growth rate, k^1					1.0

¹The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

Scorpaenidae, genus *Sebastes* (Table 6), and 5) flatfishes, Pleuronectiformes (Table 7).

All of the observed correlations agree with the predicted correlations in sign (Table 8). Of the observed correlations, 40 of a possible 46 (or 87%) were significantly different from zero at a 5% probability level. If the observed correlation agreement of coefficients were distributed ran-

TABLE 6.—Correlation matrix between life-history parameters for rockfishes (family Scorpaenidae, genus *Sebastes*). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_{∞}^1	Maximum age	Age at first maturity	k^1
Body size, L_{∞}^1	1.0	0.662 (0.019)	0.456 (0.088)	-0.490 (0.075)
Maximum age		1.0	0.612 (0.030)	-0.567 (0.040)
Age at first maturity			1.0	-0.651 (0.021)
Growth rate, k^1				1.0

¹The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 7.—Correlation matrix between the life-history parameters for flatfishes (order Pleuronectiformes). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_{∞} ¹	Maximum age	Age at first maturity	M	k ¹
Body size, L_{∞} ¹	1.0	0.755 (0.001)	0.956 (0.001)	0.291 (0.156)	-0.619 (0.005)
Maximum age		1.0	0.824 (0.001)	-0.355 (0.142)	-0.808 (0.001)
Age at first maturity			1.0	0.630 (0.014)	-0.732 (0.001)
Natural mortality, M				1.0	0.367 (0.098)
Growth rate, k ¹					1.0

¹The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 8.—Summary of the number of agreements between predicted and observed correlation coefficients among life-history parameters within selected taxonomic groups.

Level of agreement	Number in agreement	Number possible	Percent in agreement
Sign	46	46	100
5% probability level	40	46	87
1% probability level	31	46	67

domly (i.e., p = probability of agreement = 0.5, and q = probability of disagreement = 0.5), then the number of agreements would follow a binomial distribution. The binomial test (Hollander and Wolfe 1973) can be used to test the hypothesis that the number of agreements between the predicted and observed correlations differs from the number that would have occurred randomly. The number of agreements is significantly different than would have occurred randomly ($z = 4.86$, $P < 0.001$), when only correlations that were significant at the 5% level were used.

RESPONSE OF r AND K SELECTED SPECIES TO HARVESTING

The interaction of life history characteristics will have a strong affect on the response of a species to fishing pressure. The Beverton and Holt yield per recruit equation estimates the yield that can be harvested from the growth of a cohort. The model assumes that fish growth is described by the von Bertalanffy growth curve and that mortality processes are exponential (Beverton and Holt 1957; Ricker 1975). The biological parameters in the model are: 1) M , the instantaneous rate of natural mortality, 2) W_{∞} , the mean asymptotic weight which corresponds to L_{∞} , 3) k , the von Bertalanffy growth coefficient, and 4) t_{λ} , the

maximum age of a fish. From r and K selection, we can predict how these parameters will vary. Consider a situation with three hypothetical species: one species will be more r selected, another species will be more K selected, and another will be intermediate between the first two. The biological parameters will vary as shown in Table 9. Beverton and Holt yield per recruit curves were calculated for a constant age at first capture ($t_r = 4.2$ yr) with varying fishing mortality (Figure 1), and for a constant fishing mortality ($F = 0.25$) with a varying age at first capture (Figure 2).

The yield per recruit analysis points up that there are specific differences in fisheries based on r or K selected species. In fisheries based on K selected species, the maximum yield per recruit would occur at a lower level of fishing mortality and at a later age at first entry than in fisheries based on r selected species. The curves also indicate that K selected species would be much more sensitive to overfishing both in terms of fishing mortality and age at first entry.

The surplus production model of Schaefer combines reproductive and mortality functions into one parameter (Ricker 1975). The biological parameters in this model are B_{∞} , the maximum stock size (or carrying capacity in weight), and k , the instantaneous rate of increase of the stock at densities approaching zero. Again these parameters can be predicted for the three hypothetical species from r and K selection (Table 10). In the surplus production model analysis (Figure 3), the r selected species have the highest productivity. As in the yield per recruit analysis, the maximum yield occurs at a lower fishing mortality for the K

TABLE 9.—Biological parameters for use in yield per recruit analysis for three hypothetical r and K selected species.

Biological parameters	r selected species	Intermediate species	K selected species
Natural mortality, M	0.30	0.20	0.10
Mean asymptotic weight, W_{∞}	641 g	1,141 g	1,641 g
von Bertalanffy growth coefficient, k	0.22	0.14	0.07
Maximum age, t_{λ}	13 yr	20 yr	35 yr

TABLE 10.—Biological parameters for surplus production model analysis for three hypothetical r and K selected species.

Biological parameters	r selected species	Intermediate species	K selected species
Maximum stock size (B_{∞})	1.54×10^6 g	2.04×10^6 g	2.54×10^6 g
Rate of increase (k)	0.912	0.612	0.312

FIGURE 1.—The effect of different levels of fishing mortality with constant age of recruitment (4.2 yr) on yield per recruit of three hypothetical fish species demonstrating the range of r and K selection.

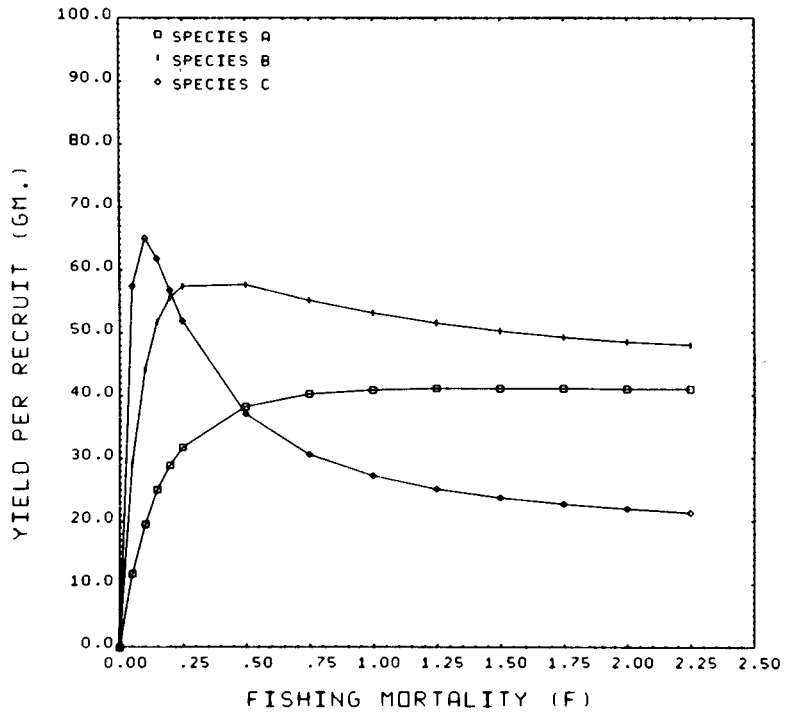
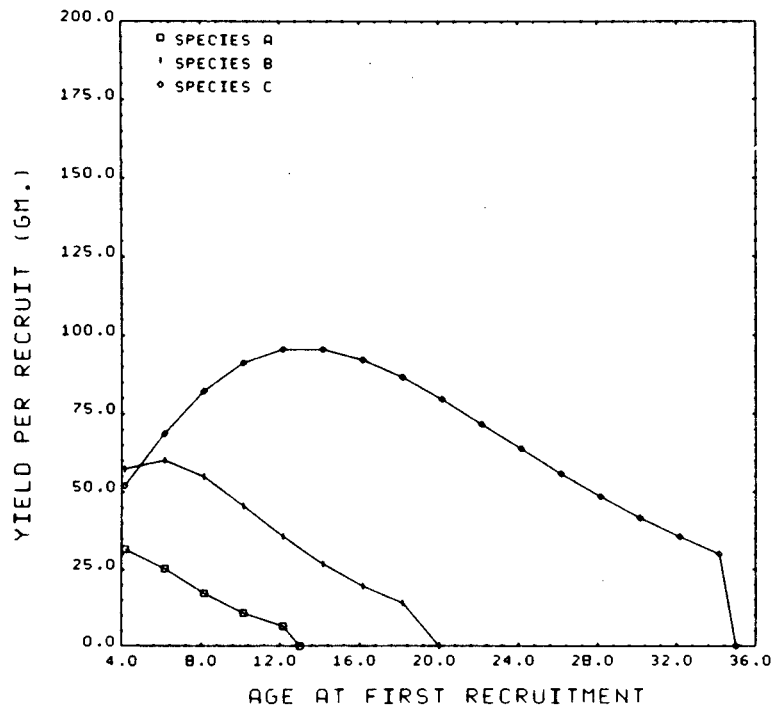


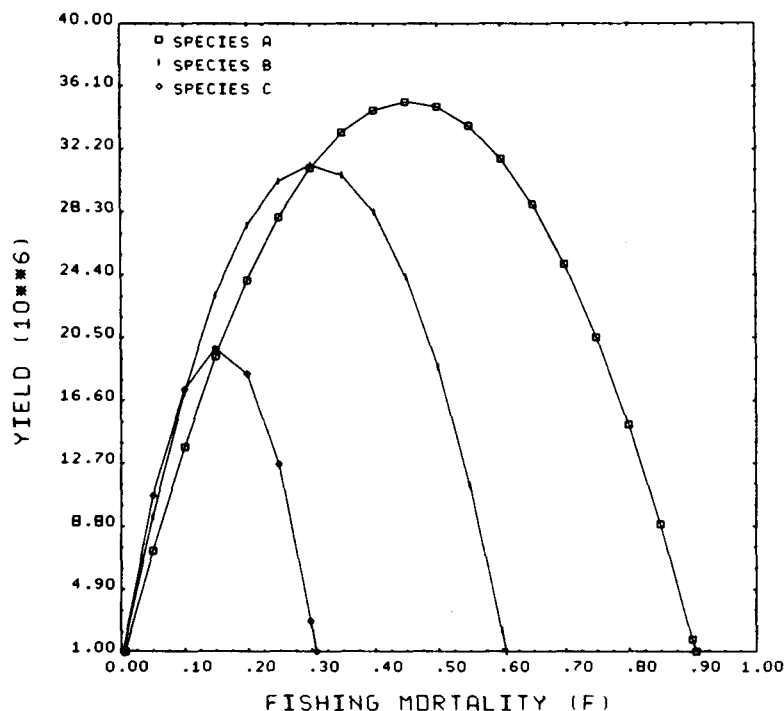
FIGURE 2.—The effect of different mean ages of recruitment at constant fishing mortality ($F = 0.25$) on yield per recruit of three hypothetical fish species demonstrating the range of r and K selection.



selected species than for the r selected species. The K selected species is reduced to levels lower than

the maximum sustainable yield by overfishing much more rapidly than the r selected species.

FIGURE 3.—Maximum equilibrium yields ($\times 10^6$ g) from Schaefer surplus production curves as a function of fishing mortality for three hypothetical fish species demonstrating the range of r and K selection.



DISCUSSION

Life history parameters vary in consistent patterns. These patterns are explainable and predictable by the theoretical constructs of r and K selection. This is not a particularly new or unique idea in fisheries biology. Beverton and Holt (1959) investigated a positive relationship between body size and life span and between mortality and growth rates. Cushing (1971) suggested that there is a negative relationship between degree of density dependent regulation and fecundity. Alverson and Carney (1975) have suggested a positive relationship between body size and the time when a cohort maximizes its biomass. In population ecology, similar relationships have been investigated for zooplankton (Allan 1976), plants (Gadgil and Solbrig 1972; MacNaughton 1975), and animals (Smith 1954; Bonner 1965). All these empirical observed trends in life history parameters, along with the trends described here, are consistent with r and K selection.

It is important to reemphasize here the comparative nature of r and K selection. The r and K continuum is a model and as such occurs only in an idealized sense. The idealized r selected species occurs in an ecological vacuum with no density

effects and no competition. The idealized K selected species occurs in a completely saturated ecosystem where densities are high compared with carrying capacities and competition for resources is intense. The problem of applying this model to any real situation is not a trivial one. Species are not simply subjected to a single selective pressure, or even to a single set of selective pressures. Because of this, r and K concepts should only be applied in a comparative sense between groups of species that have some degree of functional similarity. No species is r selected or K selected in an absolute sense; it is only relatively more r selected or K selected than some other reference species. This theory will only have value in a situation where the population dynamics of one member of a species group are fairly well understood.

The results of the model analysis give several indications about the reaction to harvesting pressure of species which are more or less r or K selected. Fisheries based on more r selected species will be more productive. They can be fished at younger ages and at higher levels of fishing mortality. Given a minimum population size, these fisheries should also have a quicker recovery from overfishing. Species which are more r

selected are likely to be strongly influenced by physical forces in the environment (Pianka 1974). Relationships of this type, e.g., between anchovies and upwelling, should be important considerations in management plans for these species.

Fisheries based on more K selected species will have a high maximum yield per recruit, but there will be fewer fish. Maximum equilibrium yield will occur at later ages of entry into the fishery and at lower levels of fishing mortality. These fisheries would be more susceptible to overfishing and stock depletion. Besides these species' sensitivity to overfishing, more K selected species are much more likely to have sophisticated life history mechanisms (Pianka 1974) which would have to be recognized in a management plan. These mechanisms might include parental care systems such as nesting or live births, mating systems, or territoriality. The more K selected species are much more likely to have strong interspecific relationships, usually competitive ones. The relationship between competition and harvesting has been dealt with by Larkin (1963) and Tanner (1975). Additional density independent mortality (fishing mortality) increases the advantage for the population with a higher population growth rate (i.e., more r selected). Therefore, even low levels of fishing pressure can destabilize a previously stable competitive pair and result in decline of the harvested species. Interestingly, the opposite result is also possible; harvesting pressure can stabilize a previously unstable species pair as Slobodkin (1962) found with experimental populations of hydra.

Fisheries based on more r selected species are likely to be of a boom and bust nature. Although in some years catches in these fisheries will be very large, they will be characterized by erratic production levels. The most efficient form of harvesting these fisheries will be fleets which are capable of switching between a number of target species relatively quickly.

Fisheries based on more K selected species, in contrast to the boom and bust nature of r selected fisheries, will be characterized by relatively stable population sizes and therefore catch levels. Given some initial measure of year class strength, possibly through larval or prerecruitment surveys, the prediction of future catches from that fishery could be made with a fair degree of accuracy. However, once fisheries based on these species become overfished, it would require a long period for the stock to rebuild to levels which can support economical

profitable fisheries. An extremely K selected species would only be suitable for trophy fisheries.

Fisheries based on r and K selected species have been discussed in a comparative sense, but predation (in the case of a fishery, human predation) will also have effects on an individual species. The gene pool of any species is going to contain within it some range of variation of both r and K selected traits. The effects of increasing fishing mortality, which is assumed to be density independent (Cushing 1975), on life history characteristics has been theoretically analyzed by Roughgarden (1971). The general effect is an increase in selective advantage for the r selected proportions of the gene pool. This would mean an increase in growth rates, reduced age at first maturity, and greater fecundity at age. These trends will be more conspicuous in species that are relatively more K selected. Species that are more strongly r selected are likely to have less range of variation in this direction. One example of these effects of predation pressure is a comparison of lake trout, *Salvelinus namaycush*, populations under heavy predation pressure from the freshwater harbor seal, *Phoca vitulina*, to populations in nearby lakes without seals (Power and Gregoire 1978). The lake trout populations which were preyed upon by seals had faster growth rates, small maximum body size, reduced maximum age, lower age at sexual maturity, and greater individual fecundity compared with populations in lakes without seals. Growth and maturation rates of certain seal species have also increased where populations have been reduced by fisheries (Sergeant 1973). These effects can be attributed to changes in selection pressure resulting from sustained harvesting.

In summary, r and K selection seems to have been an important evolutionary trend on marine fish populations. The basic hypotheses are confirmed by the data presented here. The result of patterns in population parameters which arise from r and K selection is that different management strategies would be appropriate. The value of this approach is likely to be in initial stages of development of a fishery. As a fishery becomes more developed and more specific information becomes available, a more refined management strategy would become possible.

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LITERATURE CITED

- ALANDER, H.
1950. Baltic herring. *Ann. Biol.* 6:191-192.
- ALLAN, J. D.
1976. Life history patterns in zooplankton. *Am. Nat.* 110:165-180.
- ALVERSON, D. L., AND M. J. CARNEY.
1975. A graphic review of the growth and decay of population cohorts. *J. Cons.* 36:133-143.
- ARORA, H. L.
1951. An investigation of the California sand dab, *Citharichthys sordidus* (Girard). *Calif. Fish Game* 37:3-42.
- AYUSHIN, B. N.
1963. Abundance dynamics of herring populations in the seas of the Far East, and reasons for the introduction of fishery regulations. *Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer* 154:262-269.
- BARRETT, I., AND G. V. HOWARD.
1961. Studies of the age, growth, sexual maturity and spawning of populations of anchoveta (*Cetengraulis mysticetus*) of the coast of the eastern tropical Pacific Ocean. *Inter-Am. Trop. Tuna Comm. Bull.* 5:113-165.
- BEN-TUVIA, A.
1960. Synopsis of biological data on *Sardinella aurita* of the Mediterranean Sea and other waters. In H. Rosa, Jr. and G. Murphy (editors), *Proc. World Sci. Meet. Biol. Sardines Relat. Species* 2:287-312. FAO, Rome.
- BEVERTON, R. J. H.
1963. Maturation, growth and mortality of clupeid and engraulid stocks in relation to fishing. *Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer* 154:44-67.
- BEVERTON, R. J. H., AND S. J. HOLT.
1957. On the dynamics of exploited fish populations. *Fish. Invest. Minist. Agric., Fish. Food (G.B.), Ser. II*, 19, 533 p.
1959. A review of the life spans and mortality rates in nature, and their relation to growth and other physiological characteristics. *Ciba Found. Colloq. Ageing* 5:142-177.
- BLACKBURN, M.
1950. The Tasmanian whitebait, *Lovettia seali* (Johnson), and the whitebait fishery. *Aust. J. Mar. Freshwater Res.* 1:155-198.
- BONNER, J. T.
1965. Size and cycle, an essay on the structure of biology. Princeton Univ. Press, Princeton, N.J., 219 p.
- BOUGH, P.
1952. La cruissance des poissons mediterrancius. *Vie Milieu, Suppl. 2*, 2:118-146.
- BOWERS, A. B.
1963. Recent changes in the Manx herring fishery. *Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer* 154:220-226.
- BURD, A. C.
1962. Growth and recruitment in the herring of the southern North Sea. *Fish. Invest. Minist. Agric., Fish. Food (G.B.), Ser. II*, 23(5):1-42.
- CLARK, F. N., AND J. C. MARR.
1955. Population dynamics of the Pacific sardine. *Calif. Ocean. Fish. Invest. Prog. Rep.* 1 July 1953 to 31 March 1955, p. 11-48.
- CLARK, F. N., AND J. B. PHILLIPS.
1952. The northern anchovy (*Engraulis mordax mordax*) in the California fishery. *Calif. Fish Game* 38:189-207.
- CLAYDEN, A. C.
1972. Simulation of changes in abundance of the cod (*Gadus morhua L.*) and the distribution of fishing in the North Atlantic. *Fish. Invest. Minist. Agric., Fish. Food (G.B.), Ser. II*, 27(1), 58 p.
- CROW, J. F., AND M. KIMURA.
1970. An introduction to population genetics theory. Harper and Row, N.Y., 591 p.
- CULLEY, M.
1971. The pilchard, biology and exploitation. Pergamon Press, N.Y., 241 p.
- CUSHING, D. H.
1959. On the effect of fishing on the herring of the southern North Sea. *J. Cons.* 24:283-307.
1961. On the failure of the Plymouth herring fishery. *J. Mar. Biol. Assoc. U.K.* 41:799-816.
1971. The dependence of recruitment on parent stock in different groups of fishes. *J. Cons.* 33:340-362.
1975. Marine ecology and fisheries. Camb. Univ. Press, N.Y., 278 p.
- DAVIES, D. H.
1958. The South African pilchard (*Sardinops ocellata*), preliminary report on the age composition of the commercial catches, 1950-55. Union S. Afr., Dep. Commer. Indust., Div. Fish. Invest. Rep. 33, 20 p.
- DAY, L. R.
1957. Populations of herring in the southern Gulf of St. Lawrence. In A. H. Leim, S. N. Tibbo, L. R. Day, L. Lauzier, R. W. Trites, H. B. Hachey, and W. B. Bailey, Report of the Atlantic herring investigation committee, p. 121-137. *Fish. Res. Board Can., Bull.* 111.
- DEASON, H. J., AND R. HILE.
1947. Age and growth of the Kiyi, *Leucichthys kiyi* Koelz, in Lake Michigan. *Trans. Am. Fish. Soc.* 74:88-142.
- DE JAGER, B. V. D.
1960. Synopsis on the biology of the South African pilchard, *Sardinops ocellata* (Pappé). In H. Rosa, Jr. and G. Murphy (editors), *Proc. World Sci. Meet. Biol. Sardines Relat. Species* 2:97-114. FAO, Rome.
- DICKIE, L. M., AND F. D. MCCracken.
1955. Isoleth diagrams to predict equilibrium yields of a small flounder fishery. *J. Fish. Res. Board Can.* 12:187-209.
- DRUCKER, B.
1972. Some life history characteristics of coho salmon of the Karluk River system, Kodiak Island, Alaska. *Fish. Bull. U.S.* 70:79-94.
- ELWERTOWSKI, J.
1957. Polish investigations on the sprat from the southern Baltic. *Ann. Biol.* 12:216.
1958. The sprat in the southern Baltic. *Ann. Biol.* 13:229-230.
1959. Polish investigations on Baltic sprat in 1957. *Ann. Biol.* 14:202-203.
1960. Polish investigations on sprat from the southern part of the Central Baltic - 1958. *Ann. Biol.* 15:192-193.
- FAGE, L.
1920. "Engraulidae, Clupeidae". *Rep. Danish oceanogr. Exped. Medit.*, 2(A.9). (Cited in Beverton 1963.)

- FAURE, L.
1950. Le sprat de la Baie de Douarnez pêche, biométrique et biologique. Rapp. P.-V. Réunion. Cons. Perm. Int. Explor. Mer 126:96-102.
- FLEMING, A. M.
1960. Age, growth and sexual maturity of cod (*Gadus morhua* L.) in the Newfoundland area, 1947-1950. J. Fish. Res. Board Can. 17:775-809.
- FOERSTER, R. E.
1968. The sockeye salmon, *Oncorhynchus nerka*. Fish. Res. Board Can., Bull. 162, 422 p.
- FRIDRIKSSON, A.
1950. On the herring of the north coast of Iceland during the summer of 1949. Ann. Biol. 6:162-167.
1951. On the herring and the herring fishery of the north coast of Iceland during the summer of 1950. Ann. Biol. 7:122-125.
1952. The Icelandic north coast herring in 1951. Ann. Biol. 8:136-140.
1953. The Icelandic north coast herring in 1952. Ann. Biol. 9:164-167.
1954. The Icelandic north coast herring in 1953. Ann. Biol. 10:143-147.
1956. The Icelandic north coast herring in 1954. Ann. Biol. 11:114-118.
1957. The Icelandic north coast herring in 1955. Ann. Biol. 12:158-162.
1958. The Icelandic north coast herring in 1956. Ann. Biol. 13:173-176.
1959. The Icelandic north coast herring in 1957. Ann. Biol. 14:149-154.
1960. The Icelandic north coast herring in 1958. Ann. Biol. 15:126-131.
1961. The Icelandic north coast herring in 1959. Ann. Biol. 16:163-167.
- FURNESTIN, J.
1945. "Note préliminaire sur l'anchois (*Engraulis encrasicolus* L.) du Golfe de Gascogne". Rev. Trav. Inst. Pêch. Marit. 13:197-209. (Cited in Beverton 1963.)
- GADGIL, M., AND W. H. BOSSERT.
1970. Life historical consequences of natural selection. Am. Nat. 104:1-24.
- GADGIL, M., AND O. T. SOLBRIG.
1972. The concept of *r*- and *K*-selection: evidence from wild flowers and some theoretical considerations. Am. Nat. 106:14-31.
- GILIS, C.
1957. Fall-herring concentrations exploited by the Belgian herring trawlers in 1955. Ann. Biol. 12:204-208.
1958. The Belgian herring fisheries in 1956—1957 (30 July 1956 - 19 January 1957), the North Sea - English Channel. Ann. Biol. 13:205-209.
1959. The Belgian herring fisheries in 1957—1958, the North Sea - English Channel. Ann. Biol. 14:182-188.
1960. The Belgian herring fisheries in 1958—1959. Ann. Biol. 15:176-181.
1961. The Belgian herring fisheries in 1959—1960. Ann. Biol. 16:212-215.
- HANAMURA, N.
1953. On the herring resources of Hokkaido and the South Saghalen. Bull. Jpn. Soc. Sci. Fish. 19:283-291.
- HANNERZ, L.
1956. Preliminary results of the herring investigations in the Bothnian Sea 1954. Ann. Biol. 11:156-158.
- HART, J. L.
1931. The growth of the whitefish *Coregonus clupeaformis* (Mitchell). Contrib. Can. Biol. 6:427-444.
1948. Age and growth rate in the butter sole, *Isopsetta isolepis*. Trans. R. Soc. Can., Ser. 3, Sect. 5, 42:65-72.
- HAYASHI, S.
1961. Fishery biology of the Japanese anchovy, *Engraulis japonica* (Houttuyn). Bull. Tokai Reg. Fish. Res. Lab. 31:145-268.
- HAYASHI, S., AND K. KONDO.
1957. Growth of the Japanese anchovy—IV. Age determination with use of scales. Bull. Tokai Reg. Fish. Res. Lab. 17:31-64.
- HILE, R.
1936. Age and growth of the cisco, *Leucichthys artedi* (Le Sueur), in the lakes of the northeastern highlands, Wisconsin. Bull. U.S. Bur. Fish. 48:211-317.
- HILE, R., AND H. J. DEASON.
1934. Growth of the whitefish *Coregonus clupeaformis* (Mitchell), in Trout Lake, northeastern highlands, Wisconsin. Trans. Am. Fish. Soc. 64:231-237.
- HODGSON, W. C.
1957. The herring and its fishing. Routledge & Kegan Paul, Lond., 197 p.
- HODGSON, W. C., AND I. D. RICHARDSON.
1949. The experiments on the Cornish pilchard fishery in 1947-8. Fish. Invest. Minist. Agric., Fish. Food (G.B.), Ser. M, 27(2), 21 p.
- HOLLANDER, M., AND D. A. WOLFE.
1973. Nonparametric statistical methods. Wiley, N.Y., 503 p.
- HOLT, S. J.
1962. The application of comparative population studies to fisheries biology—an exploration. In E. D. Le Cren and M. W. Holdgate (editors), The exploitation of natural animal populations, p. 51-69. Br. Ecol. Soc. Symp. 2.
- JENSEN, A. J. C.
1947. The herring at Bornholm. Ann. Biol. 2:155-158.
- KENNEDY, W. A.
1943. The whitefish, *Coregonus clupeaformis* (Mitchell), of Lake Opeongo, Algonquin Park, Ontario. Publ. Ont. Fish. Lab. 62:21-66.
1953. Growth, maturity, fecundity and mortality in the relatively unexploited whitefish, *Coregonus clupeaformis*, of Great Slave Lake. J. Fish. Res. Board Can. 10:413-441.
1954. Growth, maturity and mortality in the relatively unexploited lake trout, *Cristivomer namaycush*, of Great Slave Lake. J. Fish. Res. Board Can. 11:827-852.
- KETCHEN, K. S.
1964. Preliminary results of studies on growth and mortality of Pacific cod (*Gadus macrocephalus*) in Hecate Strait, British Columbia. J. Fish. Res. Board Can. 21:1051-1067.
- KETCHEN, K. S., AND C. R. FORRESTER.
1966. Population dynamics of the petrale sole, *Eopsetta jordani*, in waters off western Canada. Fish. Res. Board Can., Bull. 153, 195 p.
- LARKIN, P. A.
1963. Interspecific competition and exploitation. J. Fish. Res. Board Can. 20:647-678.
- LARRANETA, M. G.
1960. Synopsis of biological data on *Sardina pilchardus* of the Mediterranean and adjacent seas. In H. Rosa, Jr.

- and G. Murphy (editors), Proc. World Sci. Meet. Biol. Sardines Relat. Species 2:137-173. FAO, Rome.
- LEA, E.
1919. Age and growth of herring in Canadian waters. In J. Hjort (director), Canadian fisheries expedition, 1914-1915, investigations in the Gulf of St. Lawrence and Atlantic waters of Canada, p. 75-164. J. de Labroquerie Tache, Ottawa.
- MACARTHUR, R. H., AND E. O. WILSON.
1967. The theory of island biogeography. Princeton Univ. Press, Princeton, N.J., 203 p.
- MACKINNON, J. C.
1973. Analysis of energy flow and production in an unexploited marine flatfish population. J. Fish. Res. Board Can. 30:1717-1728.
- MACNAUGHTON, S. J.
1975. *r*- and *K*-selection in *Typha*. Am. Nat. 109:251-261.
- MENON, M. D.
1950. Bionomics of the poor-cod (*Gadus minutus* L.) in the Plymouth area. J. Mar. Biol. Assoc. U.K. 29:185-240.
- MILLER, D. J., A. E. DAUGHERTY, F. E. FELIN, AND J. MAC-GREGOR.
1955. Age and length composition of the northern anchovy catch off the coast of California in 1952-53 and 1953-54. Calif. Dep. Fish Game, Fish Bull. 101:37-66.
- MILLER, D. J., AND R. S. WOLF.
1958. Age and length composition of the northern anchovy catch off the coast of California in 1954-55, 1955-56, and 1956-57. Calif. Dep. Fish Game, Fish Bull. 106:27-72.
- MOLANDER, A. R.
1943. Sprat and milieu-conditions. Ann. Biol. 1:165-174.
- MOSHER, K. H., AND H. H. ECKLES.
1954. Age determination of Pacific sardines from otoliths. U.S. Fish Wildl. Serv., Res. Rep. 37, 40 p.
- MOTODA, S., AND Y. HIRANO.
1963. Review of Japanese herring investigations. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 154:249-261.
- MURPHY, G. I.
1966. Population biology of the Pacific sardine (*Sardinops caerulea*). Proc. Calif. Acad. Sci., Ser. 4, 34:1-84.
- NAIR, R. V.
1960. Synopsis on the biology and fishery of the Indian sardines. In H. Rosa, Jr. and G. Murphy (editors), Proc. World Meet. Biol. Sardines Relat. Species 2:329-414.
- NIELSEN, J.
1960. Preliminary results of tagging experiments with herring (*Clupea harengus* L.) in Greenland. J. Cons. 26:73-79.
- PARRISH, B. B., AND R. E. CRAIG.
1963. The herring of the north-western North Sea, post-war changes in the stock fished by Scottish drifters. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 154:139-158.
- PHILLIPS, J. B.
1948. Growth of the sardine, *Sardinops caerulea*, 1941-42 through 1946-47. Calif. Div. Fish Game, Fish Bull. 71, 33 p.
1964. Life history studies on ten species of rockfish (genus *Sebastes*). Calif. Dep. Fish Game, Fish Bull. 126, 70 p.
- PIANKA, E. R.
1974. Evolutionary ecology. Harper & Row, N.Y., 356 p.
- PINHORN, A. T.
1969. Fishery and biology of Atlantic cod (*Gadus morhua*) off the southwest coast of Newfoundland. J. Fish. Res. Board Can. 26:3133-3164.
- POSTEL, E.
1955. Résumé des connaissances acquises sur les clupéidés de l'Ouest-Africain. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 137:14-16.
- POSTUMA, K. H.
1963. The catch per unit effort and mortality rates in the Southern Bight and Channel fisheries. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 154:190-197.
- POWER, G., AND J. GREGOIRE.
1978. Predation by freshwater seals on the fish community of lower Seal Lake, Quebec. J. Fish. Res. Board Can. 35:844-850.
- POWLES, P. M.
1965. Life history and ecology of American plaice (*Hippoglossoides platessoides* F.) in the Magdalen Shallows. J. Fish. Res. Board Can. 22:565-598.
1969. Size changes, mortality, and equilibrium yields in an exploited stock of American plaice (*Hippoglossoides platessoides*). J. Fish. Res. Board Can. 26:1205-1235.
- RAITT, D. S.
1939. The rate of mortality of the haddock of the North Sea stock, 1919-1938. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 110:65-79.
- RICHARDSON, I., G. VAZZOLER, A. DE FARIA, AND M. DE MORAES.
1960. Report on sardine investigations in Brazil. In H. Rosa, Jr. and G. Murphy (editors), Proc. World Sci. Meet. Biol. Sardines Relat. Species 3:1051-1079. FAO, Rome.
- RICKER, W. E.
1949. Mortality rates in some little-exploited populations of freshwater fishes. Trans. Am. Fish. Soc. 77:114-128.
1958. Handbook of computations for biological statistics of fish populations. Fish. Res. Board Can., Bull. 119, 300 p.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. 191, 382 p.
- ROBERTSON, J. A.
1938. The sprat and the sprat fishery of England. Fish. Invest. Minist. Agric., Fish. Food (G.B.), Ser. II, 16(2), 103 p.
- ROSSIGNOL, M.
1955. Premières observations sur la biologie des Sardinelles dans la région de Pointe-Noire. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 137:16-20.
- ROUGHGARDEN, J.
1971. Density-dependent natural selection. Ecology 52:453-468.
- SCHAFFER, W. M., AND M. D. GADGIL.
1975. Selection for optimal life histories in plants. In M. L. Cody and J. M. Diamond (editors), Ecology and evolution of communities, p. 142-157. Harv. Univ. Press, Camb., Mass.
- SERGEANT, D. E.
1973. Environment and reproduction in seals. J. Reprod. Fertil. Suppl. 19:555-561.
- SHAPOVALOV, L., AND A. C. TAFT.
1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. Calif. Dep. Fish Game, Fish Bull. 98, 375 p.
- SILLIMAN, R. P.
1943. Studies on the Pacific pilchard or sardine (*Sardinops caerulea*). 5.—A method of computing mortalities and re-

- placements. U.S. Fish Wildl. Serv., Spec. Sci. Rep. 24, 10 p.
- SLOBODKIN, L. B.
1962. Growth and regulation of animal populations. Holt, Rinehart and Winston, N.Y., 184 p.
- SMITH, F. E.
1954. Quantitative aspects of population growth. In E. J. Boell (editor), Dynamics of growth process, p. 277-294. Princeton Univ. Press, Princeton, N.J.
- SMITH, W. C.
1957. Gonad condition, age and size of Manx herrings, 1945-53, and comparison with earlier years. Annu. Rep. Mar. Biol. Stn. Pt. Erin. 69:21-28.
- SOUTHWOOD, T. R. E., AND H. N. COMINS.
1976. A synoptic population model. J. Anim. Ecol. 45:949-965.
- SOUTHWOOD, T. R. E., R. M. MAY, M. P. HASSELL, AND G. R. CONWAY.
1974. Ecological strategies and population parameters. Am. Nat. 108:791-804.
- SUND, O.
1943a. The age-composition of the Norwegian spawn herring observed during 36 years. Ann. Biol. 1:45-49.
1943b. The size of the Norwegian spawn herring. Ann. Biol. 1:50-51.
- TANAKA, S.
1960. Studies on the dynamics and the management of fish populations. [In Jpn., Engl. summ.] Bull. Tokai Reg. Fish. Res. Lab. 28:1-200.
- TANNER, J. T.
1975. The stability and the intrinsic growth rates of prey and predator populations. Ecology 56:855-867.
- TAYLOR, C. C.
1958. Cod growth and temperature. J. Cons. 23:366-370.
- TESTER, A. L.
1955. Estimation of recruitment and natural mortality rate from age-composition and catch data in British Columbia herring populations. J. Fish. Res. Board Can. 12:649-681.
- TIBBO, S. N.
1956. Populations of herring (*Clupea harengus* L.) in Newfoundland waters. J. Fish. Res. Board Can. 13:449-466.
1957a. Herring of the Chaleur Bay area. In A. H. Leim, S. N. Tibbo, L. R. Day, L. Lauzier, R. W. Trites, H. B. Hachey, and W. B. Bailey, Report of the Atlantic herring investigation committee, p. 85-102. Fish. Res. Board Can., Bull. 111.
1957b. Herring populations on the south and west coasts of Newfoundland. In A. H. Leim, S. N. Tibbo, L. R. Day, L. Lauzier, R. W. Trites, H. B. Hachey, and W. B. Bailey, Report of the Atlantic herring investigation committee, p. 153-164. Fish. Res. Board Can., Bull. 111.
- TOKAI REGIONAL FISHERIES RESEARCH LABORATORY.
1960. Synopsis on the biology of *Sardinops melanosticta* (Temminck and Schlegel). In H. Rosa, Jr. and G. Murphy (editors), Proc. World Sci. Meet. Biol. Sardines Relat. Species 2:213-244. FAO, Rome.
- VAN CLEVE, R., AND D. E. BEVAN.
1973. Evaluation of causes for the decline of the Karluk sockeye salmon runs and recommendations for rehabilitation. Fish. Bull., U.S. 71:627-649.
- WATANABE, K.
1958. Growth of the anchovy in the Japan Sea. Annu. Rep. Jpn. Sea Fish. Res. Lab. 4:147-152.

APPENDIX I: LITERATURE CITATIONS FOR POPULATION PARAMETERS BY SPECIES

Herring and Anchovies, Families Clupeidae and Engraulidae

- Clupea harengus*—Lea 1919; Sund 1943a, b; Jensen 1947; Fridriksson 1950, 1951-61; Alander 1950; Tibbo 1956, 1957a, b; Hannerz 1956; Gilis 1957-61; Smith 1957; Day 1957; Cushing 1959; Nielsen 1960; Burd 1962; Parrish and Craig 1963; Postuma 1963; Bowers 1963.
- C. pallasii*—Hanamura 1953; Tester 1955; Ricker 1958; Tanaka 1960; Ayushin 1963; Motoda and Hirano 1963.
- Sprattus sprattus*—Robertson 1938; Molander 1943; Faure 1950; Elwertowski 1957-60.
- Sardinops caerulea*—Silliman 1943; Phillips 1948; Mosher and Eckles 1954; Clark and Marr 1955; Murphy 1966; Culley 1971.
- S. melanosticta*—Tanaka 1960; Tokai Regional Fisheries Research Laboratory 1960.
- S. neopilchardus*—Blackburn 1950.
- S. ocellata*—Davies 1958; De Jager 1960; Culley 1971.
- Sardina pilchardus*—Hodgson and Richardson 1949; Bough 1952; Hodgson 1957; Larrañeta 1960; Cushing 1961; Culley 1971.
- Sardinella aurita*—Postel 1955; Rossignol 1955; Richardson et al. 1960; Ben-Tuvia 1960; Beverton 1963.
- S. longiceps*—Nair 1960.
- Engraulis encrasicolus*—Fage 1920; Furnestin 1945.
- E. japonicus*—Hayashi and Kondo 1957; Watanabe 1958; Tanaka 1960; Hayashi 1961.
- E. mordax mordax*—Clark and Phillips 1952; Miller et al. 1955; Miller and Wolf 1958; Culley 1971.
- Cetengraulis mysticetus*—Barrett and Howard 1961.

Salmons, Family Salmonidae

- Coregonus clupeaformis*—Hart 1931; Hile and Deason 1934; Kennedy 1943, 1953; Ricker 1949.
Cristivomer namaycush—Kennedy 1954.
Leucichthys artedii—Hile 1936.
L. kiyi—Deason and Hile 1947.
Oncorhynchus kisutch—Shapovalov and Taft 1954; Drucker 1972.
O. nerka—Foerster 1968; Van Cleve and Bevan 1973.

Cods, Family Gadidae

- Boreogadus saida*—Beverton and Holt 1959.
Gadus callarias—Beverton and Holt 1957; Taylor 1958.
G. macrocephalus—Ketchen 1964.
G. minutus—Menon 1950.
G. morhua—Fleming 1960; Pinhorn 1969; Clayden 1972.
G. virens—Beverton and Holt 1959.
Melanogrammus aeglefinus—Raitt 1939; Beverton and Holt 1957.
Merluccius merluccius—Beverton and Holt 1959.

Rockfishes, Family Scorpaenidae,
Genus *Sebastodes*

- Sebastodes crameri*—Phillips 1964.
S. diploproa—Phillips 1964.
S. entomelas—Phillips 1964.
S. flavidus—Phillips 1964.
S. goodei—Phillips 1964.
S. jordani—Phillips 1964.
S. miniatus—Phillips 1964.
S. paucispinis—Phillips 1964.
S. pinniger—Phillips 1964.
S. saxicola—Phillips 1964.

Flatfishes, Order Pleuronectiformes

- Citharichthys sordidus*—Arora 1951.
Eopsetta jordani—Ketchen and Forrester 1966.
Hippoglossus platessoides—Powles 1965, 1969; MacKinnon 1973.
H. vulgaris—Beverton and Holt 1959.
Isopsetta isolepis—Hart 1948.
Pleuronectes platessa—Beverton and Holt 1959.
Pseudopleuronectes americanus—Dickie and McCracken 1955.
Solea vulgaris—Beverton and Holt 1957.