Hadlow, Eds. (Academic Press, New York, 1979), vol. 2, p. 387.
83. J. A. Rose, *Compr. Virol.* **3**, 1 (1974); F. L. Schaffer and C. E. Schwerdt, *Adv. Virus Res.* **6**, 159 (1959).
84. T. O. Diener and W. B. Raymer, *Virology* **37**, 351 (1969).
85. T. O. Diener, *Viroids and Viroid Diseases* (Wiley, New York, 1979).
86. H. L. Sänger, K. Ramm, H. Domdey, H. J. Gross, K. Henco, D. Riesner, *FEBS Lett.* **99**, 117 (1979).
87. E. Mihalyi, *Application of Proteolytic Enzymes to Protein Structure Studies* (CRC Press, Cleveland, 1972).
88. S. B. Prusiner, J. Cleaver, D. F. Groth, unpublished observations.
89. A. D. McLaren and D. Shugar, *Photochemistry of Proteins and Nucleic Acids* (Pergamon, New York, 1964).
90. J. J. Butzow and G. L. Eichhorn, *Biopolymers* **3**, 95 (1964); *Nature (London)* **254**, 358 (1975).
91. S. T. Isaacs, C. J. Shen, J. E. Hearst, H. Rapoport, *Biochemistry* **16**, 1058 (1977).
92. M. P. McKinley, F. R. Masiarz, J. Hearst, S. B. Prusiner, in preparation.
93. J. E. Hearst and L. Thiry, *Nucleic Acid Res.* **4**, 1339 (1977); C. V. Hanson, J. L. Riggs, E. H. Lennette. *J. Gen. Virol.* **40**, 345 (1978).
94. C. Hanson, personal communication.
95. D. Crowther and J. L. Melnick, *Virology* **14**, 11 (1961).
96. K. Borgert, K. Koschel, H. Taüber, E. Wecker, *J. Virol.* **8**, 1 (1971).
97. P. Bornstein and G. Balian, *J. Biol. Chem.* **245**, 4854 (1970).
98. R. M. Franklin and E. Wecker, *Nature (London)* **184**, 343 (1959); E. Freese, E. Bautz-Freese, E. Bautz, *J. Mol. Biol.* **3**, 133 (1961); H. Schuster and H.-G. Wittman, *Virology* **19**, 421 (1963); J. H. Phillips and D. M. Brown, *Prog. Nucleic Acid Res. Mol. Biol.* **7**, 349 (1967); I. Tessman, *Virology* **35**, 330 (1968).
99. T. Alper, D. A. Haig, M. C. Clarke, *J. Gen. Virol.* **41**, 503 (1978).
100. ———, *Biochem. Biophys. Res. Commun.* **22**, 278 (1966).
101. R. Latarjet, R. Cramer, L. Montagnier, *Virology* **33**, 104 (1967); J. S. Semancik, T. J. Morris, L. G. Weathers, *ibid.* **53**, 448 (1973).
102. J. A. Reynolds, in *Membrane Receptors*, S. Jacobs and P. Cuatrecasas, Eds. (*Receptors and Recognition*, Series B, vol. 11) (Chapman & Hall, London, 1981), p. 33.
103. P. Andrews, *Methods Biochem. Anal.* **18**, 1 (1971); Y. Nozaki, N. M. Schechter, J. A. Reynolds, C. Tanford, *Biochemistry* **15**, 3884 (1976).
104. A. C. T. Nozth and A. Rich, *Nature (London)* **191**, 1242 (1961); C. Tanford, *Physical Chemistry of Macromolecules* (Wiley, New York, 1961), pp. 317–456.
105. R. Langridge, H. R. Wilson, C. W. Hooper, M. H. F. Wilkins, L. D. Hamilton, *J. Mol. Biol.* **2**, 19 (1960); G. Giannoni, F. J. Padden, Jr., H. D. Keith, *Proc. Natl. Acad. Sci. U.S.A.* **62**, 964 (1969); W. C. Earnshaw and S. R. Casjens, *Cell* **21**, 319 (1980).
106. V. W. Yang, M. R. Lerner, J. A. Steitz, S. J. Flint, *Proc. Natl. Acad. Sci. U.S.A.* **78**, 1371 (1981).
107. J. M. K. Mackay, *Nature (London)* **219**, 182 (1968); I. H. Pattison, K. M. Jones, J. N. Jebbett, *Res. Vet. Sci.* **12**, 30 (1971).
108. J. M. Bishop, *Cell* **23**, 5 (1981).
109. W. O. Weigle, in *Autoimmunity: Genetic, Immunologic, Virologic and Clinical Aspects* (Academic Press, New York, 1977), p. 141; B. H. Waksman, *Clin. Exp. Immunol.* **28**, 363 (1977); L. F. Qualtiere and P. Meyers, *J. Immunol.* **122**, 825 (1979).
110. F. Crick, *Nature (London)* **227**, 561 (1970).
111. R. Craig, *J. Theor. Biol.* **88**, 757 (1981); H. Kleinkauf and H. Von Dahren, *Curr. Top. Microbiol. Immunol.* **91**, 129 (1981).
112. W. M. Stanley, *Science* **81**, 644 (1935).
113. C. J. Gibbs, Jr., D. C. Gajdusek, H. Amyx, in *Slow Transmissible Diseases of the Nervous System*, S. B. Prusiner and W. J. Hadlow, Eds. (Academic, New York, 1979), vol. 2, p. 87; E. E. Manuelidis and L. Manuelidis, in *ibid.*, p. 147; J. Tateishi, M. Ohta, M. Koga, Y. Sato, Y. Kuroiwa, *Ann. Neurol.* **5**, 581 (1979); D. T. Kingsbury, D. A. Smeltzer, H. L. Amyx, C. J. Gibbs, Jr., D. C. Gajdusek, in preparation.
114. A. G. Dickinson and H. Fraser, in *Slow Virus Infections of the Central Nervous System*, V. ter Meulen and M. Katz, Eds. (Springer-Verlag, New York, 1977), p. 3; R. H. Kimberlin and C. A. Walker, *J. Gen. Virol.* **39**, 487 (1978).
115. S. B. Prusiner, S. P. Cochran, D. F. Groth, D. Hadley, H. Martinez, W. Hadlow, in *Aging of the Brain and Dementia*, L. Amaducci, A. N. Davison, P. Antuono, Eds. (Raven, New York, 1980), p. 205.
116. W. J. Hadlow, unpublished observations; R. P. Hanson, R. J. Eckroade, R. F. Marsh, G. M. Zu Rhein, C. L. Kanitz, D. P. Gustafson, *Science* **172**, 859 (1971).
117. G. Allen and K. H. Fantes, *Nature (London)* **287**, 408 (1980); S. Nagata, N. Mantei, C. Weissmann, *ibid.* **287**, 401 (1980); M. Rubinstein *et al.*, *Arch. Biochem. Biophys.* **210**, 307 (1981).
118. A. G. Dickinson and H. Fraser, in *Slow Transmissible Diseases of the Nervous System*, S. B. Prusiner and W. J. Hadlow, Eds. (Academic Press, New York, 1979), vol. 1, p. 367.
119. D. T. Kingsbury and J. D. Watson, in preparation.
120. This article is dedicated to Dr. Francis A. Sooy on the occasion of his completing a decade as Chancellor of the University of California, San Francisco. I thank F. Elvin, F. R. Masiarz, L. Gallagher, S. P. Cochran, D. F. Groth, M. P. McKinley, K. A. Bowman, D. E. Downey, N. I. Mock, D. P. Stites, and J. R. Baringer for continuing help in these studies; Drs. R. C. Williams, R. C. Morris, Jr., P. Bendheim, D. Bolton, T. O. Diener, W. J. Hadlow, A. Gordon, H. Fields, B. M. Alberts, T. B. Kornberg, I. F. Diamond, W. J. Rutter, M. Rubinstein, and R. M. Stroud for discussions during the preparation of this manuscript; and Drs. F. Seitz, R. Schmid, L. H. Smith, Jr., and J. R. Krevans for support and encouragement. Supported by NIH research grants NS14069 and AG 02132, NSF grant PCM77-24076, a gift from the R. J. Reynolds Industries, and past funds from the Howard Hughes Medical Institute.

Dominance in Fishes: The Relation Between Environment and Abundance

Bernard Einar Skud

Marine fishery studies are replete with comparisons of environmental factors and population abundance or recruitment, and, recently, correlation matrices have been used to compare responses (coefficients) of different species to the same factor (*1, 2*). Although the studies have included dominant and subordinate species that interact (*3, 4*), the responses of these species have not been related specifically to their positions in the dominance hierarchy. The purposes of this articles are to compare the relation of temperature to the catch of Atlantic herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*), species that have alternated as dominant and subordinate in the pelagic biomass off New England and the Canadian Maritime Provinces, and to relate their response to dominance. The relation also is examined for other species, including the California sardine (*Sardinops sagax caerulea*) and anchovy (*Engraulis mordax*).

To paraphrase Daan (*5*), the dominant species is defined as the more abundant of two species that have a functional relation (interact) and whose densities are maintained at distinctly different levels. He specified that replacement, or a change in dominance, required at least a 50 percent reduction in abundance of one stock and a comparable increase in the other and that the change be persistent for a number of years.

Interaction Between Herring and Mackerel

Landings (catch) and other estimates of abundance and biomass of herring and mackerel in the Gulf of St. Lawrence since 1960 indicated that the species interact and have alternated as the dominant species in the pelagic biomass (*4, 6*). The evidence was based on 15 years of data and on the results obtained from simulation models. The estimates of abundance were from cohort analyses and recruitment surveys. The conclusions of the investigators (*4, 6*) were tempered by the constraints of their models and by the need for a longer series of empirical data. Supporting evidence of this interaction is apparent in data from Georges Bank (*7*) and from the North Sea (*8*).

In order to satisfy the need for a long-term empirical series I compared the landings of mackerel and herring from the Gulf of Maine to the Gulf of St. Lawrence from the late 1800's to 1960 (Fig. 1) (*9, 10*). I assumed that long-term

---

The author is a marine biologist with the National Marine Fisheries Service in Narragansett, Rhode Island 02882, an adjunct professor of Oceanography at the University of Rhode Island, and president of the American Institute of Fishery Research Biologists.

0036-8075/82/0409-0144$01.00/0

trends in landings represented major fluctuations in abundance and tested this assumption (*10*). My basic premise was that a truly competitive relation would transcend the deficiencies of the landings data and that it was the relative difference in the abundance of the two species that was critical to the determination of an interaction.

Mackerel statistics were available from 1815 in the United States and from 1876 in Canada. From 1850 to 1880 the United States catch averaged 45,000 metric tons annually, and the maximum during this period was 66,000 metric tons in 1851. Herring statistics were not available before 1873, but narrative accounts of the fisheries showed that the supply of herring was low during much of the 1800's and that herring had to be imported from Newfoundland to meet the demand for bait and salted products in New England (*11*). The evidence suggested that mackerel dominated the pelagic biomass during most of the 1800's. With the unexplained collapse of the mackerel fishery in the 1880's, the landings indicate that herring attained dominance by 1890 and retained that position until the late 1960's (*10*). Apparently, either the increase in the abundance of herring contributed to the decline of mackerel or the reduced competition from mackerel permitted the increase in the abundance of herring.

The continued low catch of mackerel throughout the 1900's, even though fishing effort was reduced and temperatures were favorable, and the negative correlation of herring and mackerel landings support the conclusion that the two species interact as shown in the Gulf of St. Lawrence (*4*, *6*). Further support is evident in estimates of biomass (*12*) for the northwestern Atlantic since 1960. When the abundance of herring declined, mackerel reattained dominance.

The mechanism or mechanisms controlling the interaction between herring and mackerel have not been indentified (*3*, *4*, *13*, *14*). The species are known to compete for some food resources and are cannibalistic. Further, the juvenile and adult stages of both species prey on larvae and postlarvae of the other species, so that the role of prey and predator changes with increasing size. Both species are preyed upon heavily by demersal fishes. For these reasons and because the mechanisms change with life history stages and their effects have not been quantified, I use competition in its broadest sense, to include any action by one species that adversely affects the survival of the other, including predation.

Summary. Changes in abundance of dominant species of fish were positively correlated with environmental factors that improved survival, and abundance of the subordinate species was negatively correlated with the same factors. When dominance changed, the responses of both the dominant and subordinate species also changed. Implicit in this inverse relation is the conclusion that the abundance of the subordinate depends on the density of the dominant species, and this hierarchy must be recognized in the interpretation of the correlations. Changes in dominance not only explained why the response of a species changed from positive to negative, but also why different stocks did not respond in the same way to temperature. The findings support the thesis that climatic factors can affect the abundance of a species but do not govern its absolute population density. The results have important implications for fishery management.

Temperature, Abundance, and Dominance

Laboratory studies (*15*) showed that the effects of temperature on herring differ with respect to stocks, spawning time, egg size, and salinity, but the development and survival of herring eggs and larvae improve as temperatures increase. Similar results were obtained for mackerel (*16*).

Taylor, Bigelow, and Graham (*17*) correlated temperatures with U.S. landings of mackerel and obtained a positive and statistically significant relation from 1820 to 1890. They found, however, that the correlation from 1890 to 1954 was insignificant and stated that there was little evidence of any relation with temperature during the latter period. In these comparisons, mean annual temperatures were compared with landings 3 years later. I reexamined the data, confirmed the findings, and noted that herring dominated the pelagic landings after 1890. Further, whereas herring landings before 1900 were mainly adults, the landings of juveniles (sardines) increased consistently and by 1909 accounted for approximately 90 percent of the herring catch (*9*). During this transition period, landings of neither species showed a strong relation to temperature, but the correlation between temperature and mackerel landings from 1909 to 1960 was negative and statistically significant (Table 1). Taylor *et al.* (*17*) used air temperatures from New Haven, Connecticut, for their comparisons. These data were closely correlated with sea-surface temperatures before 1930, but the relation deteriorated thereafter. And I found that the data were negatively correlated with sea-surface temperatures during the 1940's, when the weather station was moved from the city to the airport, and the method of calculating the daily mean had been changed. I used these data for comparisons before 1909; thereafter I used sea-surface temperature data from Boothbay Harbor, Maine (available since 1906), which were positively and significantly correlated with other sea-surface temperature records for the North Atlantic.

During the mid- and late 1960's, the biomass of mackerel in the northwestern Atlantic was increasing, whereas herring was decreasing (*12*). By the early 1970's, the biomass of mackerel was twice that of herring. Fishing mortality (instantaneous rate) of mackerel increased markedly during this period and increased from 0.268 to 0.626 in the years 1971 to 1976 (*18*). With this high exploitation the abundance of mackerel declined rapidly, and neither species was dominant in the late 1970's. Anderson and McBride (*19*) correlated the year-class strength of mackerel at age 1 with temperature from 1961 to 1972 and obtained a negative correlation. Mackerel was the subordinate species during most of this period. To examine the period immediately before and after herring lost dominance, I compared temperature and mackerel biomass at age 1 for the northwestern Atlantic from 1965 to 1971 and obtained a negative correlation, and from 1972 to 1976, when mackerel were dominant, I obtained a positive correlation (Table 1). These results indicate that correlations spanning a change in dominance are misleading because the correlations in the component years were of the opposite sign.

There is other evidence of a change in sign during component years.

In the Gulf of St. Lawrence, the relation of temperature to the abundance of mackerel was positive from 1961 to 1971 (*3*, *4*). This period included a change in dominance. The biomass of herring recruits was more than twice that of mackerel until 1967; thereafter mackerel biomass exceeded herring. I compared temperature with biomass of mackerel recruits before and after 1967 and also divided the period into seven early and seven late years. Again, correlations during component years of a period spanning a change in dominance were negative and positive (Table 1). These results, and more specifically those for the period before 1960, indicate that the relation of temperature to the abundance of mackerel was positive when mackerel was dominant and negative when mackerel was subordinate.

Several investigators (*1*, *20*) have reported positive correlations between sea-surface temperatures and the landings of herring in the Gulf of Maine. These studies encompassed the period from 1928 to 1971, when herring dominated the catch of pelagic fish in the area. Using data from earlier periods (*9*), I found that from 1884 (peak mackerel catch) to 1908, the period of transition of dominance from mackerel to herring, and from adult herring to juveniles, the correlation of temperature with abundance of herring was not statistically significant. After 1908 and until 1960, the correlation was positive and statistically significant. I obtained a similar result from 1928 to 1960, when U.S. data were available in consecutive years and Canadian data were available from the southern Gulf of St. Lawrence (Table 1). After 1960 the catch increased when a fishery for adult herring was established on Georges Bank. Herring lost dominance in the late 1960's. To examine the relation with temperature during this period, I used estimates of stock size of herring (*21*) and compared them with annual mean temperatures 3 years earlier. The sign of the correlation changed when dominance changed (Table 1).

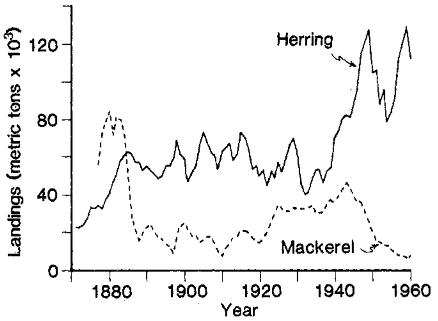

Fig. 1. Landings of herring and mackerel in Canada and the United States. The data are smoothed by a moving average of 3's (*9*).

Data from the Gulf of St. Lawrence (*3*, *4*) indicated that the relation of temperature to recruit herring was negative from 1963 to 1971. Dominance changed during this period, the correlation for the years before 1967 was negative and was positive after 1967 (Table 1). I also compared the temperature data from Entry Island, Quebec (*22*), with estimates of adult biomass from the Gulf of St. Lawrence (*23*) and obtained similar results.

The correlations between abundance and temperature for both species indicate that the dominant species responds positively and the subordinate species negatively. Because of the reciprocal response to temperature and because the landings of the two species are negatively correlated, I conclude that the abundance of the dominant species governs the abundance of the subordinate species and that the effects of competition mask the actual response of the subordinate to temperature. The results also indicate that comparisons of responses of different species can lead to totally erroneous interpretations if this hierarchy is ignored. A negative response by a subordinate species is apparently a reaction to a change in the abundance of the dominant species and not to the effects of the physical environment. To test this thesis I examined interactions of other species, for which estimates of abundance other than commercial landings were available.

Table 1. Correlations (*r*) between abundances of herring (H) and mackerel (M) and temperature. Abundance estimates for the first four periods were landings; estimates for the other periods were based on virtual population analyses. Mackerel landings were from all areas; herring landings from the southern Gulf of St. Lawrence were not included before 1928. Periods for comparison were determined by changes in dominance or availability of data: 1884 was the peak of mackerel landings; sea-surface temperatures became available in 1909, when juveniles accounted for 90 percent of the herring landings; and U.S. data on herring were sporadic before 1928. Results for the northwestern Atlantic and the southern Gulf of St. Lawrence after 1960 are presented to show that correlations which span a change in dominant species have a negative and positive component.

Period	Dominant species	Mackerel		Herring	
		r	Number of years	*r*	Number of years
		Air temperature			
1820 to 1884 (U.S.)	M	+.492*	65		
1885 to 1908	H	−.043	24	+.066	16
		Sea-surface temperature			
1909 to 1960	H	−.405*	52	+.459*	40
1928 to 1960	H	−.743*	33	+.627*	31
		Northwest Atlantic			
1965 to 1976	HM	−.422	12	−.429	12
1965 to 1971	H	−.732	7	+.451	7
1972 to 1976	M	+.513	5	−.580	5
		Southern Gulf of St. Lawrence (Canada)			
1963 to 1971	HM	+.261	9	−.116	9
1963 to 1967	H	−.618	5	+.705	5
1968 to 1971	M	+.886	4	−.874	4
1963 to 1969	H	−.382	7	+.820†	7
1965 to 1971	M	+.535	7	−.204	7

*$P < .01$. †$P < .05$.

Environmental Factors and Dominance

Evidence of the effect of dominance in relation to environmental factors is also apparent in the interaction of sardines and anchovies in California. The correlation between sardine recruitment and salinity was positive ($r = .845$; $P < .01$) from 1934 to 1941, and negative ($r = .639$; $P < .05$) from 1942 to 1955 (*24*). The sardine was dominant during the early period, and its recruitment declined steadily after 1940. The anchovy attained dominance during the latter period. The relation of abundance to temperature also changed. I compared the catch and catch per unit of effort with sea-surface temperatures (Table 2) (*25*). The responses of the two species to temperature differed and changed with dominance, as did the responses of herring and mackerel. The responses of sardine and anchovy to temperature were inverse to those of salinity. Temperature and salinity are associated with upwelling and are themselves inversely related (*24*). Bakun (*26*) computed annual upwelling indices for the California coast. The correlation coefficients (*r*) of the index at 36°N and 122°W with the abundance of sardine and anchovy larvae from 1951 to 1959 were −.630 and +.592, respectively. Apparently, salinity or related environmental factors such as food and nutrients improved the growth or survival of the adults, whereas the effects of temperature were not critical. However, during the larval stages, temperature did affect survival and the dominant species responded positively. This difference in the responses by larvae and adults may explain the inconsistencies in the relation of year-class strength of sardines to stock size (*27*).

I also reviewed studies on freshwater fishes for similar effects of dominance. Nilsson (*28*) and Svärdson (*29*) discussed the evidence of dominance in Scandinavian lakes. Their studies showed that changes in dominance were associated with significant ecological changes such as the introduction of new species, conversion of lakes to reservoirs, acidification, and eutrophication. Nilsson (*30*) showed that certain species in Scandinavian lakes had different habitat and food preferences when they were competing, but their preferences were similar when the species occurred separately. Svärdson (*29*) reported that dominant species were regulated mainly by environmental (abiotic) factors or intraspecific competition, whereas the abundances of subordinate species were influenced more by interspecific competition for food or by predation. My findings are in general agreement with his.

I also compared the relation of dominance to temperature using the experimental data of Silliman (*31*). Control and test tanks were exposed to similar temperature regimes. Temperature and biomass for each of 75 periods were based on 3-week means. The brood interval for guppy (*Poecilia reticulata*) was 3 weeks and for swordtail (*Xiphorphorus maculatus*) 4 weeks. I compared the biomass of a period with the temperature of the previous period. In the control (no exploitation), guppy was dominant from periods 13 to 28. The correlation between temperature and swordtail biomass was +.658 ($P < .01$) and for guppy −.652 ($P < .01$).

In the test tank, the exploitation rates at the beginning and the end of the experiment usually exceeded 25 percent and the fluctuations in biomass were severe. The most stable periods were from 33 to 65, when exploitation was below 25 percent most of the time. Swordtail was dominant, and its biomass was at least twice that of guppy until period 61. However, the numbers of the two species were about the same from period 47 to 58, indicating that the swordtails were mainly adults and the guppies mainly juveniles. The correlation with temperature from periods 33 to 47 was −.492 for swordtail and +.825 ($P < .01$) for guppy; and from periods 33 to 65, −.495 for swordtail and +.269 for guppy. The decrease in the statistical significance of the correlation for guppy suggests that abundance as well as biomass is important in determining dominance. The signs of the correlations in the test tank were the opposite of those in the control tanks, where guppy was dominant. (The negative relations between the dominant species and temperature indicate that temperatures during the experiments were at or above the optimum for population growth.)

Table 2. Correlations (*r*) of temperature and indices of abundance of sardines (S) and anchovies (A). Catch and catch per unit of effort (CPUE) were used for adults and numbers per unit of water strained for larvae.

Period	Number of years	Dominant species	*r* (sardine)		*r* (anchovy)	
			CPUE	Catch	CPUE	Catch
			Adults			
1932 to 1939	8	S	−.421	−.410		+.353
1940 to 1947	8	A	+.649	+.520		−.655
1941 to 1959	19	A		+.863*		−.560†
			Larvae			
1951 to 1959	9	A	−.710†		+.801*	

$*P < .01$. $†P < .05$.

The changes in dominance between herring and mackerel and the other interacting species explained why correlations between temperature and abundance failed and may explain the failure of correlations between environmental factors and abundance of other species. Bell and Pruter (*32*), warning about fortuitous relations, reviewed examples of correlations that have failed, and Gulland (*33*) noted how few relations have stood the test of time. Their cautions about correlation analyses and their interpretations still pertain. However, my data on dominance show that a change in response is not acceptable evidence that a climatic factor did not affect abundance or that the observed relation was spurious. Nor is it valid, before considering dominance, to dismiss a correlation for one species when a competing species has not shown a similar response or if the same species did not respond in the same way in a different area. These conclusions do not imply that all correlations that fail are the result of a change in dominance.

In commercial fisheries, fishing mortality usually reduces the abundance of the dominant species below its equilibrium density. Because of their economic importance, these dominant species generally are studied most intensively, and therefore it is not surprising that their fluctuations in abundance have frequently been correlated with changes in the environment. This emphasis on dominant species may explain why the inverse responses of subordinate species have not been detected. The lack of attention to subordinate species supports the argument (*34*) for an ecosystem approach to population dynamics. I suspect that the effects of dominance are equally applicable to competing stocks of the same species and for competing groups within a stock: for example, competition between the spring and fall spawning stocks of herring in the Gulf of St. Lawrence (*10*).

Control of Population Abundance

Svärdson (*29*) suggested that the type of population control was species-specific for some species and that ". . . evolution would mould two different types of fish, depending on whether intra- or interspecific competition is the most forceful agent. . . ." Larkin (*35*) reviewed the evidence on interactions in freshwater environments and concluded that ". . . in some aquatic habitats and for some species of fish, climatic controls would seem to outweigh biological factors in controlling population . . ." but that in environments characterized by physical stability ". . . biological factors would undoubtedly be involved as population controls. . . ." Watt (*36*) said that productivity of a species could be governed by one or the other or both controls depending on whether the species was located in the center or near the boundaries of its range. He cited smallmouth bass (*Micropterus dolomieu*) as being regulated largely by temperature in north temperate zones and suggested that in southern areas intra- and interspecific competition controlled the populations. In contrast, LeCren (*37*) concluded that ". . . the normal high levels of spawning and heavy juvenile losses are doubtless connected with the operation of density-independent mortality which tends to cause large fluctuations in survival . . . [and] that density-independent mortality factors will normally obscure the operation of density-dependent factors, but in the long run the latter will be important for the maintenance of stable populations, both in natural and fished stocks. . . ."

The observed effects of alternation of dominance indicate that the usual type of control is not species-specific, nor is it determined by the relative stability of the environment or by distribution within the species' range. Although factors such as climate can cause large fluctuations in survival, I relate the high potential fecundity and high juvenile losses to density-dependent factors. Density is governed by the carrying capacity of the ecosystem and the species' apparent response to climatic change is dependent on its position in the dominance hierarchy and its population size relative to its equilibrium density. Lower densities at the boundaries of a species' range may frequently be determined by other species that are more suitably adapted to the particular climatic regime.

The species-specific explanations of population control (*29, 35*) are not unlike conclusions reviewed by Pielou (*38*) that species are adapted to succeed at either intra- or interspecific competition or are controlled by either density-independent or -dependent factors. Pielou questioned how widely the generalizations of the *r*- or *K*-selection theory applied to the marine environment. Because dominance influences the interactions and responses of certain fishes, dominance should be considered before population characteristics are identified with natural selection and these characteristics are specified as ecological strategies.

Solomon (*39*) stressed that the performance of a population was dependent on both abiotic and biotic factors and made a distinction between their relative importance to population control. He separated general control from the controlling processes and argued that, in the general sense, physical factors of the environment were of primary importance and biotic factors secondary. The physical factors not only determined whether a species could exist in a particular place but also influenced the vigor, rate of development, power of survival, and the levels of metabolism and activity. In contrast, he said that biotic elements were predominant in the controlling processes although not independent of the abiotic factors. Nicholson's (*40*) laboratory experiments with insects were concerned mainly with the controlling processes, and he considered populations as self-governing systems that regulated their densities in relation to their own properties and those of the environment. He concluded that climatic conditions had a "legislative" role and were ultimately responsible for the composition of the community, but that climate could not determine absolute density and that intraspecific competition was the usual mechanism governing density.

My results, showing the changes in the relation between abundance and physical factors of the environment with changes in dominance, support Nicholson's thesis concerning the role of abiotic factors. The trends in abundance of the dominant and subordinate species support his conclusions regarding intraspecific competition but also show the significance of interspecific interactions which he had included as a part of the environment. Nicholson did describe patterns of fluctuations in abundance of predator and prey populations that were characterized by cyclic oscillations. In accordance with his thesis, the trends in abundance would indicate that one of the species periodically exceeded its equilibrium density. Populations held below their equilibrium densities, such as the exploited species that I examined, did not exhibit cyclic fluctuations. The effects of exploitation and the interactions of dominant and subordinate species have implications for population assessment and to the management of fisheries (*3, 4, 10*) as well as the management problems discussed by May *et al.* (*41*).

What are the mechanisms that control the interactions? How are they effective for species that occupy different niches and usually do not intermingle? Not enough quantitative information is available to provide definitive answers to these questions, and I shall not review the arguments concerning mechanisms such as predation and competition for food. However, the Scandinavian studies on dominance emphasized the probable importance of competition for space, a mechanism seldom considered in the interactions of marine fishes. Svärdson (*29*) and Nilsson (*30*) reported changes in habitat and food preferences when species were subordinate and that dominance of freshwater fishes differed with lake size and depth. Their results suggest that it is not a question of how the interaction works when the competing species occupy different niches, rather that the difference is a result of the interaction.

I propose that the density-dependent factors that govern recruitment of a species also function in an interspecific mode to control the abundance of competing species and to determine dominance. A change in dominance, such as occurred for herring and mackerel in the 1960's, was coincident with changes in recruitment. When the recruitment of both species was low and neither was dominant in the 1970's, Sherman *et al.* (*42*) reported a 20-fold increase in the larvae of sand launce (*Ammodytes* spp.), suggesting that density-dependent factors control the composition of the pelagic biomass. Ricker (*43*) said that density measurements are needed for each age group to fully describe the effect of stock abundance on recruitment, and this requirement may also be the key to the understanding of multispecies interactions.

Conclusions

Changes in abundance of dominant and subordinate fishes in response to changes in the physical environment showed that dominant species responded positively to factors that improved their survival, and subordinate species responded negatively to the same factors. The responses changed when dominance changed. This inverse relation indicates that the abundance of the subordinate species is controlled by the abundance of the dominant species.

If this hierarchy is ignored, the interpretation of a correlation between the abundance of a subordinate species and an environmental factor may be erroneous because interspecific interactions may mask the actual relation. Changes in dominance explained why a species, in one area, responded positively to temperature for many years and then responded negatively, and why a species, in different geographical areas, did not respond in the same way to temperature. Correlations that fail should not be summarily dismissed as spurious until changes in dominance are considered. Dominance should be examined when responses of either the same or closely associated species in different years or areas are compared.

The maintenance of distinct levels of abundance for two interacting species suggests that exploitation reduces the biomass of the dominant species below its equilibrium density, enabling it to respond to favorable climatic factors. If competition is reduced through a reduction in the biomass of the dominant species, the subordinate is capable of increasing through intraspecific interactions even though climatic factors may not be entirely favorable. The dependence of the subordinate abundance on that of the dominant species would explain the lack of a stock-recruitment relation for certain species.

The inverse relation of the abundance of the dominant and subordinate species to physical factors in the environment and the observed changes in dominance support Nicholson's (*40*) thesis that climatic factors can affect the abundance of a species but do not govern its absolute density and that the mechanism controlling abundance within a population is intraspecific competition. In addition to its bearing on ecological concepts of population control, the effects of dominance have particular significance to problems in fishery management.

References and Notes

1. W. H. Sutcliffe, K. Drinkwater, B. S. Muir, *J. Fish. Res. Board Can.* **34**, 19 (1977).
2. D. J. Garrod and J. M. Colebrook, *Rapp. P.-V. Reun. Cons. Int. Explor. Mer* **173**, 128 (1978).
3. P. F. Lett, A. C. Kohler, D. N. Fitzgerald, *Int. Comm. Northwest Atl. Fish. Res. Doc. 33*, (1975), p. 1.
4. G. H. Winters, *J. Fish. Res. Board Can.* **33**, 1751 (1976).
5. N. Daan, *Rapp. P.-V. Reun. Cons. Int. Explor. Mer*, in press.
6. P. F. Lett and A. C. Kohler, *J. Fish. Res. Board Can.* **33**, 1838 (1976).
7. S. H. Clark and B. E. Brown, *Fish. Bull.* **75**, 1 (1977); R. C. Hennemuth, J. E. Palmer, B. E. Brown. *Cons. Int. Explor. Mer Annu. Meet. Doc H:57* (1979), p. 43.
8. E. S. Russell, *U.K. Board Agric. Fish. Fish Invest. Ser. III* (1915), p. 1; M. J. Holden, *Rapp. P.-V. Reun. Cons. Int. Explor. Mer* **172**, 11 (1978).
9. For herring, only Canadian statistics [A. G. Huntsman, *J. Fish. Res. Board Can.* **10**, 1 (1953)] were available for consecutive years since 1870. The catches of both countries in the early years were made in Passamaquoddy Bay. For Fig. 1, the Canadian data were doubled to account for missing U.S. data before 1928. The U.S. catch actually exceeded that of Canada in 18 of 26 years during this period. For correlations with temperature, only those years were used for which catches were reported by both countries. United States and later Canadian herring statistics are from L. W. Scattergood and S. N. Tibbo [*Bull. Fish. Res. Board Can.* **121**, 42 (1959)], V. C. Anthony [thesis, University of Washington (1972)], and C. H. Lyles [*U.S. Fish. Wildl. Serv. Stat. Dig.* **59**, 756 (1967)]. Mackerel statistics are from O. E. Sette and A. W. H. Needler [*U.S. Bur. Fish Invest. Rep.* **19**, 48 (1934)] and from annual reports of fishery agencies.
10. B. E. Skud, in preparation. My analysis was limited to the period before 1960; after that fishing changed drastically because of foreign fishing in the western North Atlantic. Before 1960, only Canadian and United States fishermen harvested the stocks of herring and mackerel. Anthony [in (*9*)] found close agreement between the catch per unit of effort of stop-seine gear and the total catch of herring from Maine. He concluded that catch usually was representative of year-class strength but that abundant year-classes could be underestimated when the supply exceeded the demand or the capacity of the canneries. M. T. Sinclair, T. D. Iles, and W. Sutcliffe [*Int. Comm. Northwest Atl. Fish. Res. Doc. 80/IX/139:NP* (1980)] found statistically significant relations between the catch rate by age (1 to 3 years) from Canadian herring weirs with estimates of year-class strength from 1964 to 1975. The United States catch of mackerel during the 1960's showed the same trends as four different indices of abundance described by E. D. Anderson [*Int. Comm. Northwest Atl. Fish. Res. Bull.* **12**, 5 (1976)].
11. R. E. Earll, *U.S. Comm. Fish Fish.* **1**, 417 (1887); G. B. Goode, "The fishery industries of the United States" (U.S. Commission on Fish and Fisheries, Washington, D.C., 1888), vol. 1, p. 1; L. W. Scattergood and S. N. Tibbo, in (*9*).
12. Northeast Fisheries Center, National Marine Fisheries Service, Woods Hole, Mass., unpublished data.
13. K. T. MacKay, *Can. Fish. Mar. Serv. Tech. Rep. 885* (1979), p. 26.
14. R. Maurer, *Int. Comm. Northwest Atl. Fish. Res. Doc. 3967* (1976), p. 22.
15. J. H. S. Blaxter and F. G. T. Holliday, *Adv. Mar. Biol.* **1**, 261 (1963); J. H. S. Blaxter and G. Hempel, *J. Cons. Cons. Perm. Int. Explor. Mer* **2**, 211 (1963).
16. L. G. Worley, *J. Gen. Physiol.* **16**, 841 (1933).
17. C. C. Taylor, H. B. Bigelow, H. W. Graham, *U.S. Fish Wildl. Serv. Fish. Bull.* **57**, 289 (1957).
18. E. D. Anderson, *Cons. Int. Explor. Mer Annu. Meet. Doc. H:40* (1977), p. 26.
19. E. D. Anderson and M. M. McBride, *Int. Comm. Northwest Atl. Fish. Res. Doc. 16/12/139* (1976).
20. V. C. Anthony, in (*9*); R. L. Dow, *J. Cons. Cons. Int. Explor. Mer* **37**, 274 (1977).
21. V. C. Anthony and G. T. Waring, *Northwest Atl. Fish. Org. Doc. 135* (1980), p. 38.
22. L. M. Lauzier, and J. H. Hull, *Fish. Res. Board Can. Tech. Rep.* **150**, 5 (1969).
23. D. M. Ware and B. L. Henriksen, *ibid.* **800**, 83 (1978).
24. The correlation in the early period was reported by L. A. Walford [*J. Mar. Res.* **6**, 48 (1946)] and in the later period by J. Marr [*FAO (F.A.O.U.N.) Proc. World Sci. Meet. Biol. Sardines* **III**, 667 (1960)]; G. A. Bogdanov [*Probl. Ichthyol. (U.S.S.R.)* **8**, 695 (1968)] recognized the change as one of paramount importance and hypothesized that temperature was the critical factor and that it was related to salinity and upwelling.
25. The temperature and catch-per-unit-effort data are from J. Radovich [*Calif. Fish Game Fish. Bull.* **112**, 62 (1961)]; the catch data are from G. I. Murphy [*Fish Population Dynamics*, J. A. Gulland, Ed. (Wiley, New York, 1977), p. 283], and the data on larvae are from E. H. Ahlstrom [*Int. Comm. Northwest Atl. Fish. Spec. Publ.* **6**, 53 (1965)].
26. A. Bakun, *U.S. Natl. Mar. Fish. Serv. Tech. Rept. SSRF-671* (1973), p. 103.
27. F. N. Clark and J. C. Marr, *Calif. Coop. Ocean. Fish. Invest. Rep. 1953–55* (1955), p. 11.
28. N. A. Nilsson, *J. Fish. Res. Board Can.* **29**, 693 (1972).
29. G. Svärdson, *Fish. Board Swed. Inst. Freshwater Res. Drottningholm* **55**, 144 (1976).
30. N. A. Nilsson, in *Biological Basis of Freshwater Fish Production*, S. D. Gerking, Ed. (Wiley, New York, 1967), p. 296.
31. R. P. Silliman, *Fish. Bull.* **73**, 872 (1975).
32. F. H. Bell and A. T. Pruter, *J. Fish. Res. Board Can.* **15**, 625 (1958).
33. J. A. Gulland, *Int. Comm. Northwest Atl. Fish. Spec. Publ.* **6**, 363 (1965).
34. M. D. Burkenroad, *Publ. Inst. Mar. Sci. Univ. Tex.* **2**, 177 (1951); J. L. McHugh, *Trans. Am. Fish. Soc.* **88**, 105 (1959); R. L. Edwards, *FAO (F.A.O.U.N.) Fish. Rep.* **171**, 91 (1975).
35. P. A. Larkin, *J. Fish. Res. Board Can.* **13**, 327 (1956).
36. K. E. F. Watt, in *Exploitation of Natural Animal Populations*, E. D. LeCren and M. W. Holdgate, Eds. (Wiley, New York, 1962), p. 191.
37. E. D. LeCren, in *ibid.*, p. 283.
38. E. C. Pielou, *Ecological Diversity* (Wiley, New York, 1975), p. 165.
39. M. E. Solomon, *J. Anim. Ecol.* **18**, 1 (1949).
40. A. J. Nicholson, *Aust. J. Zool.* **2**, 9 (1954).
41. R. M. May, J. R. Beddington, C. W. Clark, S. J. Holt, R. M. Laws, *Science* **205**, 267 (1979).
42. K. Sherman, C. Jones, L. Sullivan, W. Smith, P. Berrien, L. Ejsymont, *Nature (London)*, in press.
43. W. E. Ricker, *Bull. Can. Dept. Environ. Fish. Mar. Serv.* **191**, 382 (1975).
44. I thank C. M. Jones, University of Rhode Island; W. E. Hazen, San Diego State University; K. S. Ketchen and W. E. Ricker, Pacific Biological Station, Nanaimo, British Columbia; P. A. Larkin, University of British Columbia; J. Paloheimo, University of Toronto; L. W. Scattergood, Arlington, Va.; R. P. Silliman, Seattle, Wash.; staff members of the Northeast Fisheries Center, National Marine Fisheries Service, for reviewing the manuscript; and R. G. Quayle, National Weather Service, and J. B. Colton, National Marine Fisheries Service, for information concerning temperature records.