where A is the coefficient matrix of the canonical representation of the system shown in Eq. 3:

$$dx_{1}/dt = a_{11}x_{1} + a_{12}x_{2} + \dots + a_{1n}x_{n} + b_{1} = 0$$

$$dx_{2}/dt = a_{21}x_{1} + a_{22}x_{2} + \dots + a_{2n}x_{n} + b_{2} = 0$$

$$\dots \dots \dots \dots \dots \dots$$

$$dx_{m}/dt = a_{m1}x_{1} + a_{m2}x_{2} + \dots + a_{mn}x_{m} + b_{n} = 0$$
 (3)

and X is a column vector whose components are the variables x_1, x_2, \ldots, x_n x_n . Since it is usually not possible to obtain sufficient data to represent natural ecosystems canonically and since they are probably not linear, formal stability criteria are not generally available for ecological applications. The only realistic approach is to develop empirical measures. MacArthur (2) has provided such a measure for food webs, relating their stability to their entropy. A stability criterion for nvariable ecosystems is formulated below and applied to the variables of the York River listed in Table 1. The primary data are fully reported elsewhere (3) with details of the methods employed.

In considering the stability of plankton, two basic problems are (i) how stable are they and (ii) are they more stable than their immediate environment? If all the variables of an ecological system were random variables, randomly sampled, then each variable might be regarded as most stable if and when the probability for an increase in value when low and for a decrease when high were unity. Assuming the stability of the whole system to be in direct relation to that of the individual variables (not a sound assumption, technically, but acceptable for first approximation purposes), then a simple stability measure might be

$$=\frac{1}{n}\sum_{j=1}^{n}s_{j} \qquad (4)$$

where σ is the stability of the system, and s_i that of the *j*th of *n* variables. For stability of the separate variables, consider the matrix of transition probabilities P:

σ

$$P = \begin{bmatrix} p_{id}p_{ii}\\ p_{dd}p_{di} \end{bmatrix}$$
(5)

where p_{id} represents the probability for a decrease following an increase, p_{ii} that for an increase following an increase, and so forth. We may associate with P a determinant, and employ it as a stability measure for the *j*th variable. Thus, Eq. 4 can be written

$$\sigma = \frac{1}{n} \sum_{j=1}^{n} \det P_j$$
 (6)

where σ has a range $-1 \leq \sigma \leq 1$. Null stability of the system is denoted by $\sigma = 0$, instability by $\sigma < 0$, and stability by $\sigma > 0$.

By separating all the variables of the York River for which data were obtained into two groups, physical and biological stabilities can be computed separately for the environment (σ_E) and for the plankton (σ_P) . The calculations are summarized in Table 1. The results, $\sigma_E = 0.12$ and $\sigma_P = 0.65$, indicate that the plankton were 5.4 times more stable than the physical habitat. This degree of homeostasis (0.65 on a scale with maximum value unity) seems quite remarkable considering how loosely integrated plankton communities are usually thought to be (4).

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Table 1. Stability determinations for plankton in the York River during the summer of 1960. "Trajectory" refers to the line of behavior of each variable (averaged for the whole water column) in terms of whether it increased (i) or decreased (d) over the preceding observation.

Variables (j)	Trajectory	P_{id}	P_{di}	P_{ii}	P_{dd}	det P_j
	Environme	nt				
Temperature	iiidididd	.60	.67	.40	.33	.27
Chlorinity	iiiiidddi	.20	.33	.80	.67	- 47
Dissolved oxygen	iddiiddid	.75	.50	.25	.50	25
Nitrate-nitrogen	diidddid	.67	.50	33	50	17
Inorganic phosphorus, dissolved	diiddiidi	.50	.75	.50	.25	.25
Inorganic phosphorus, adsorbed	iddiiiidd	.40	.33	.60	.67	- 27
Organic phosphorus, dissolved	iiddidddd	.67	.20	.33	.80	- 13
Total solids	ididdiidi	.75	.75	.25	.25	.50
Extinction coefficient	ididdiidd	.75	.50	.25	.50	.25
Secchi disc	didiiddii	.50	.67	.50	.33	.17
Light intensity	dddididdd	1.00	.33	.00	.67	.33
$\Sigma \det P_j$						1.32
$\sigma_E = \frac{1}{11} \Sigma \det P_j$						0.12
	Plankton					
Total chlorophyll	dididid	1.00	1.00	00	00	1.00
Chlorophyll <i>a</i> *	idiiidid	.60	1.00	40	.00	60
Chlorophyll b*	didiidid	.75	1.00	.25	.00	.00
Chlorophyll c*	(none present)				.00	.15
Carotenoids, astacin*	ididiidi	.75	1.00	.25	.00	75
Carotenoids, non-astacin*	(none present)					
Organic phosphorus, particulate	iddidiiid	.60	.67	.40	.37	.25
Biomass	ididdiddi	1.00	.60	.00	.40	.60
Cell counts	iididid	.80	1.00	.20	.00	.80
Number of species	didiididi	.75	1.00	.25	.00	.75
Gross production	iidididid	.80	1.00	.20	.00	.80
Respiration	iddiiidid	.60	.67	.40	.33	.25
Net production	diiididid	.60	1.00	.40	.00	.60
$\Sigma \det P_j$						7.15
$\sigma_P = \frac{1}{11} \sum \det P_j$						0.65
* Information provided by M. L. Brehm	ner.					

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Bow Wave Riding of Dolphins

Abstract. Dolphins riding bow waves were observed through underwater viewing ports. The postures assumed by the dolphins show that they present their bodies rather than the ventral surfaces of their flukes to the propellant forces of the bow wave.

How dolphins ride bow waves is the subject of a current controversy. After observing them performing this feat through underwater viewing ports in a ship's bow, I would like to report the method the dolphins themselves seem to consider proper.

Since Woodcock (1) noticed the "motionless" swimming of dolphins and interpreted it as bow wave riding, several proposals attempting to reconcile it with hydrodynamic theory have been advanced. Woodcock and McBride (2) concluded that only under conditions of laminar flow and nonbuoyancy could a dolphin sufficiently overcome drag to get a ride. Hayes (3) then showed in

a terse presentation of calculations of hydrodynamic forces that the buoyancy of a dolphin in a pressure gradient determined the amount of hydrodynamic lift needed but did not affect the drag. Approaching the problem experimentally, Scholander (4) concluded that the tail flukes of a dolphin in the incline of a bow wave and properly angled up into the incline would be subject to enough force to push the whole animal forward. Objections by Hayes (5) to Scholander's hypothesis and a rebuttal by Scholander (6) were printed in Science. A point in disagreement was whether the forward component of the bow wave forces acted on the entire dolphin or just on its flukes. Fejer and Backus (7), stating that Hayes's explanation was correct but incomplete, supplied more observations on porpoises and computations on the nature of the pressure field and the function of ship's length and drag coefficient on the position of a wave-riding porpoise.

Underwater observation ports installed in the bow of the Charles H. Gilbert (Fig. 1)-research ship of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii-in early 1960 for the purpose of studying tuna behavior provided excellent facilities for observing and photographing dolphins riding the bow wave. Since that time I have had occasion to observe several species of dolphins off the coast



Fig. 2. Postures of Tursiops sp. while riding a bow wave.

of northern California, off the coast of Mexico, and near Kingman Reef in the central equatorial Pacific. Motion pictures were successfully taken at the last location.

Porpoises did not always find the bow wave suitable for riding. When they first approached, they swam from side to side in front of the ship for a few minutes, apparently testing the pressure field, before they engaged in wave riding or left.

The field observations and reviews of the movie show that the dolphins assume several attitudes. The range of postures they assumed while riding the bow wave of the ship, which traveled at about 9 knots is shown in the outline drawings taken directly from the film (Fig. 2). The posture shown in Fig. 2B is the one most commonly



Fig. 1. Underwater viewing ports in the bow of the Charles H. Gilbert.

seen. The trailing edge of the flukes was an estimated $\frac{1}{2}$ to 3 feet ahead of bow. The position and predominant posture of the dolphins indicate that their bodies are used to take advantage of the forward component of the forces of the bow wave. Moreover, they were never seen riding with their flukes angled in conformance with Scholander's hypothesis. The flukes seemed to be used solely to control hydrodynamic lift.

Although the dolphins often rode steadily, without changing their positions relative to the bow wave, they seem to prefer weaving laterally in and out among each other. In doing so they continually changed their vertical positions by as much as 3 feet and thus exhibited excellent control of hydrodynamic lift and stability by changing the planes of their pectorals and flukes, bending their bodies, and banking. Implied in Hayes's explanation is the necessity of lift control to enable the dolphins to meet exigencies caused by buoyancy changes. Therefore, although such control was postulated (6, 8) to support Scholander's hypothesis, this assumption also supports Hayes's explanation (9).

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