

The constraints on cephalopods: why squid aren't fish

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The convergent evolution of cephalopods and fish has often been discussed on an anatomical basis, but recent advances in the knowledge of cephalopod life cycles, physiology, and biochemistry suggest that there are constraints on cephalopods that prevent them from competing directly with fish. These advances are reviewed against the background of detailed information on fish from the perspective that the basic inefficiency of the jet-propulsion system has required bioenergetic, physiological, and biochemical adaptations in squid which maximize their metabolic rates. Such "high-energy" adaptations are suggested to have resulted in the short life history and semelparous reproductive patterns that seem to characterize these coleoid cephalopods. Conversely, the physiology and biochemistry of fish give them distinct advantages for long lives and iteroparity.

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L'évolution convergente des céphalopodes et des poissons a souvent fait l'objet de discussions basées sur l'anatomie des organismes, mais, plus récemment, l'acquisition de connaissances sur les cycles biologiques des céphalopodes, leur physiologie et leur biochimie indique que des contraintes empêchent les céphalopodes de faire une compétition directe aux poissons. Ces nouvelles données sont révisées à la lumière des données disponibles sur les poissons en tenant compte que l'inefficacité inhérente au système de déplacements par propulsion a obligé les céphalopodes à développer des adaptations bioénergétiques, physiologiques et biochimiques propres à maximiser leur taux de métabolisme. De telles adaptations à coût énergétique élevé ont probablement donné lieu au cycle biologique court et au mode de reproduction semelpare qui semble caractériser ces céphalopodes coléoides. Inversement, la physiologie et la biochimie des poissons donnent lieu à une vie longue et un mode de reproduction itéropare.

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Introduction

In his 1972 review, "Cephalopods and fish: the limits of convergence," Packard examined the ecology, anatomy, and physiology of these two groups from the perspective that "cephalopods functionally are fish" and used the comparison to argue that this convergence was the result of competition for the same niche. Since its publication this article has become a "touchstone" for cephalopod research because of its comprehensive overview. This period has been a very active one in the field, and many of the biochemical, physiological, and ecological questions Packard raised have now been looked at in detail. Major symposia (Nixon and Messenger 1977; Balch et al. 1978; Recksiek and Frey 1978; Roper et al. 1983; Rowell and Nigmatullin 1985), expeditions (Hochachka 1976; Arnold 1982), Wells' treatise on octopus physiology (1978), Boyle's volumes on cephalopod life cycles (1983 and 1986), and a series of chapters devoted exclusively to cephalopods in *The Mollusca* (Arnold 1983; Boucaud-Camou and Boucher-Rodoni 1983; Gosline and Shadwick 1983a; Hochachka et al. 1983; Storey and Storey 1983; Summers 1983; Wells 1983) have brought much of this work together, but no attempt has been made to look at the new data in Packard's original context.

Our article will compare nektonic squids and fishes, in part because they exhibit the most convergence, but also because the squid literature is most in need of review. Although, taxonomically, the terms fish and squid apply to everything from seahorses to floating jelly blobs, for most people they produce a mental image very close to *Salmo* and *Loligo*; such classical forms are the focus of the article. It will emphasize those aspects of biochemistry and physiology in which squid and fish differ most and will largely ignore the literature on the giant axon and the visual pigment systems, which have been very extensively

studied and reviewed. For the sake of brevity, it will, in many cases, only refer the reader to recent reviews where these are adequate. For the fish comparisons, too, it will draw primarily on secondary sources such as the *Fish Physiology* series edited by Hoar and Randall since 1969. Our view of the very concept of convergence has changed somewhat since 1972. The vogue for optimality theory first led us to believe that there might be only one "best" way to exist in a particular habitat, but later recognized that organisms might not be evolving toward universal optima but were rather more likely to become trapped in a "local" optimum dictated by constraints (Stearns 1984).

To clarify why certain aspects of squid physiology and biochemistry might be constrained, it would help to know the group's evolutionary origins. These are far from clear, but recent work on the "living fossils" of the genus *Nautilus* gives considerable insight into how the ancestors of the coleoids may have functioned. There are dangers in extrapolating back 400 million years, but there is reasonable evidence that the "life styles" of the nautiloids have not changed dramatically in that time (Ward 1983a). A brief look at some similarities and major contrasts between these two cephalopod groups will, at least, focus on the most likely constraints. The living nautiloids are solitary epibenthic predator/scavengers, making extensive daily vertical excursions, generally in association with vertical reef surfaces. Their heavy shells are supported with air-filled chambers but still permit only limited pelagic swimming, probably largely for escape. They neither feed nor make extensive horizontal migrations pelagically (Ward et al. 1984). *Nautilus* spp. also deposit very large (ca. 25 mm) eggs in the substrate, which produce miniature adult offspring after nearly a year of development (Arnold and Carlson 1986). This pattern of reproduction may account for the limited distribution of the

group. Perhaps reflecting the large eggs and high juvenile survival inside the heavy protective shell, the nautiloids grow slowly, have long lives, and reproduce iteroparously (Saunders 1984).

Although typical squids also have separate sexes and, as predators, consume a live diet of similar chemical composition, they differ from their ancestors in most other respects. They spend much of their lives in open water moving vertically hundreds of metres daily and thousands of kilometres in seasonal migrations. Seasonal migrations appear primarily to ensure that planktonic offspring will be in suitable places to take advantage of rich food supplies (Harden Jones 1980). There is some variation in reproductive patterns between the myopsids (e.g., *Loligo*), which typically attach thousands of eggs to the substrate, and the oegopsids (e.g., *Illex*), which spawn hundreds of thousands of eggs pelagically; however, both groups produce much smaller eggs than the nautiloids and have juveniles that are distributed by currents. All squid with known life cycles grow rapidly, live less than 2 years, and are essentially semelparous.

The failure of squid to take advantage of the wide variety of reproductive tactics used by fish is the single most remarkable example of the constraints on the group. Stearns (1984) has commented on this and suggested that perhaps the limitation results from an endocrine system incapable of producing multiple cycles, based on evidence for "programmed senescence" in octopuses (Wodinsky 1977). Calow (1986) argues that, given the wide variety of reproductive tactics in other molluscs, this seems improbable and suggests that the programmed senescence is more likely a consequence of selection for fast growth rates in young cephalopods. Rapid growth would reduce the likelihood of juvenile mortality due to predation, since juveniles would be small and vulnerable for a shorter time. This, in turn, would make high adult investments in reproduction and semelparity less risky since the probability of offspring surviving would be high. This article will review the physiological and biochemical features of squid that may have resulted in their being optimized to "live fast and die young," in contrast to fish, which grow more slowly and reproduce repeatedly. The theme, then, is that while both fish and squid have a similar "style of life" there are marked differences in their "pace of life."

The origin of this difference must lie in the selection pressures that produced the coleoids from their ancestors. As indicated, these origins cannot be traced precisely, but the coleoids are more closely related to the ammonoids than the nautiloids (Dzik 1981). The ammonoids produced lighter, stronger shells and smaller eggs and their enormous radiation suggests that they produced planktonic juveniles and were successful colonizers, probably even of the open ocean (Landman et al. 1983). Why the ammonoids vanished at the end of the Cretaceous remains unclear. However, many families had disappeared before the end, suggesting that the group was already declining and may have been under severe competitive pressure (Ward 1983b). The major radiations of the teleosts and squid also occurred during the Cretaceous, and these increasingly mobile forms may have displaced the ammonoids while competing with each other. This suggests a scenario of competition between several groups producing small eggs and planktonic offspring where speed and agility were pitted against protective armor. If the beginnings of the convergence of fish and squid arose from this selection for locomotory prowess, it should be appropriate for the review to begin with a look at recent studies of the locomotory energetics of the two groups.

Bioenergetic limitations

Jet swimming

The extensive literature on fish locomotion and energetics, dating back over 50 years, has been recently reviewed (Blake 1983; Beamish 1978; Magnuson 1978; Webb 1978) and gives a relatively comprehensive background for the present comparison. The quantitative literature on squid locomotion dates from Trueman and Packard's (1968) comparative study of jet pressures in several cephalopods and has been recently reviewed by Trueman (1980, 1983). Both groups gain forward momentum by accelerating water backwards, but most fish undulate through the water, pushing large volumes back at low speeds while jetting squid can only accelerate the water they take into their mantles. To gain equivalent momentum, squid must accelerate this water to much higher speeds. Much of the energy invested in this acceleration is not recovered as momentum, resulting in a low Froude efficiency (Alexander 1977). Some semibenthic squid use their fins extensively, and all squid use them to some extent for hovering and maneuvering; however, "classic" squid depend on the jet at all speeds and cannot even hover without it (O'Dor and Balch 1985). There are, as yet, no analyses of the relative contributions of jet and fins at various speeds. There are, however, good records of tagged squid *averaging* speeds between 0.30 and 0.37 m s⁻¹ for weeks at a time (e.g., Hurley and Dawe 1980), and, at the speeds necessary to attain these averages, the fins are rolled up against the body to reduce drag for much of the time (Webber 1985; O'Dor 1982). Low Froude efficiency is clearly a significant factor during major portions of the lives of most squid.

In squid the pressure-volume work that drives the process comes from contraction of the circular muscles of the mantle wall, which pressurizes the mantle cavity. Johnson et al. (1972) have shown that reasonable estimates of jet thrust can be made knowing only the pressure and the area of the funnel aperture. Thrust is directly proportional to pressure and generally predictive of the swimming speeds of cephalopods (Table 1). Although squid achieve accelerations more than 10 times those of *Nautilus* and equal to those of fish, Table 2 shows that their sustained swimming speeds are only half of those of comparable fish because their power output is discontinuous. Their efficiency is also lower; calculations indicate that the Froude efficiency of *L. opalescens* is less than one-third that of a similar sized trout (Alexander 1977). There is no way around this fundamental inefficiency of the jet propulsion system. Although there are some compensations such as lower drag because squid can maintain a streamlined shape unlike undulatory fish, the best performing squid studied to date still uses more than twice as much energy to travel half as fast as an average fish (Webber and O'Dor 1985). Fish that swim by oscillation of the caudal fin, like tuna, probably do even better. Apparently the only thing that keeps squid in the competition is the fact that the jet system automatically increases water flow over the gills as swimming speed increases. Even without cell-bound respiratory pigments, squids manage to consume oxygen at the highest rates ever observed for aquatic poikilotherms at comparable sizes and temperatures.

The problem of efficiency is not limited to high speeds. Figure 1 shows the energetic cost of transporting a unit mass of organism over unit distance at optimum speeds (i.e., speeds at which cost is minimal). The fish are still about four times as efficient as adult squid. Interestingly, however, the limited evidence available suggests that the cost of transport (*C*) may scale differently in the two groups. Schmidt-Nielsen (1971)

TABLE 1. Comparative burst swimming performance for cephalopods and a typical fish with data on jet-system characteristics

	<i>Nautilus macromphalus</i> ^a	<i>Octopus vulgaris</i>	<i>Sepia officinalis</i>	<i>Loligo opalescens</i> ^b	<i>Loligo vulgaris</i>	<i>Illex illecebrosus</i> ^c	<i>Salmo gairdneri</i> ^d
Weight (g)	690	220	250	40	350	500	250
Burst speed (m/s)	0.2	—	0.8	1.0	2.0	2.8	2.7
Acceleration (m/s ²)	—	—	—	8	32	39	36
Jet frequency (Hz)	1.25	—	3.0	1.5	2.0	0.8	—
Mantle volume (% body weight)	8	15	25	45	50	45	—
Peak pressure (kPa)	4	20	20	22	30	50	—
Thrust (N)	0.4	1.0	3.5	1.4*	5.0	8.4	—

NOTE: All data from Trueman and Packard 1968 or Trueman 1980 except as noted by superscripts: (a) Packard et al. 1980; (b) O'Dor, unpublished observations; (c) Webber 1985 and unpublished observations; (d) Beamish 1978 and Webb 1978.

*This thrust (T) was calculated according to the equation discussed by Johnson et al. (1972): $T = C_d a P$. The coefficient of discharge (C_d) was assumed to be 1.0, and the area of the funnel aperture (a) and the peak pressure during a jet cycle (P) were measured. Other thrusts were measured directly but shown to correspond reasonably well with calculated values by Trueman and Packard (1968).

TABLE 2. Performance and metabolic rates of squid and fish during sustained swimming

	<i>Oncorhynchus nerka</i> ^a	<i>Illex illecebrosus</i> ^b	<i>Loligo pealei</i> ^c	<i>Loligo opalescens</i> ^d
Temperature (°C)	15	15	22	14
Total length (m)	0.37	0.42	0.24	0.20
Mass (g)	500	400	100	40
Critical speed (m/s)	1.35	0.76	0.60	0.36
Active metabolism (mL O ₂ kg ⁻¹ h ⁻¹)	480	1047	950	862
Standard metabolism (mL O ₂ kg ⁻¹ h ⁻¹)	40	313	320	254
Resting metabolism (mL O ₂ kg ⁻¹ h ⁻¹)	—	202	300	239
Scope for activity (mL O ₂ kg ⁻¹ h ⁻¹)	440	734	630	608
Gross cost of transport (J kg ⁻¹ m ⁻¹)	1.9	7.6	9.6	12.6
Net cost of transport (J kg ⁻¹ m ⁻¹)	1.7	5.4	6.1	7.7
Oxygen debt (mL kg ⁻¹)	329	167	—	73

NOTE: Data from: (a) Brett 1965; (b) Webber and O'Dor 1985; (c) Freadman et al. 1984 and personal communication; (d) O'Dor 1982. Definitions as given by Brett 1965 and O'Dor 1982. Metabolism for squid resting on the bottom is lower than extrapolated metabolism at zero speed (standard metabolism) because they are negatively buoyant.

showed that C generally decreases with animal weight (W) according to the equation, $C = aW^b$ and a regression analysis of Brett's (1965) data for sockeye salmon, *Oncorhynchus nerka*, gave $b = -0.3$. For the three studied species of squid, ranging from 20 to 600 g, a similar regression gives $b = -0.2$. Although one would normally hesitate to extrapolate from such limited data, Schmidt-Neilsen found that his regression fits most undulatory swimmers, including bull sperm. There are no good data on the cost of transport for squid smaller than those in Table 2, but O'Dor et al. (1986) made estimations based indirectly on oxygen consumption measurements by Hurley (1976) which were consistent with the lower slope for jet swimmers. There is, as yet, no hydromechanical analysis or even an established theoretical basis to support these empirical observations, but there are interesting consequences if the trends hold. At sizes on the order of milligrams or less, jet propulsion may be more efficient than undulation, which could be a major factor in the evolutionary scenario discussed above. Fortunately for the squid and fish that eat them, the paddling crustaceans appear to

be less efficient at all sizes, based on both empirical (Torres 1984) and analytical evidence (Morris et al. 1985). This suggests that adult squid should not only invest heavily in their offspring because they have high growth rates, which reduce the likelihood of mortality as suggested by Calow (1986), but also because the offspring are more competitive energetically relative to fish than the adults themselves.

Direct measurement of locomotion costs in juvenile squid have so far proved impossible, largely because they do not orient and swim steadily in a current, but Packard (1969) showed that weight-specific power output increases 25-fold as *Loligo vulgaris* grows from 1 to 100 g. There have also been significant advances from the theoretical approach. The model Johnson et al. (1972) presented appears reasonable for adults during a single jet, but neglects such important factors in sustained swimming as the acceleration reaction (the added energy cost of accelerating the animal and boundary layer water during unsteady swimming) discussed by Daniel (1983) in his model for medusae, the energy provided by the radial muscles

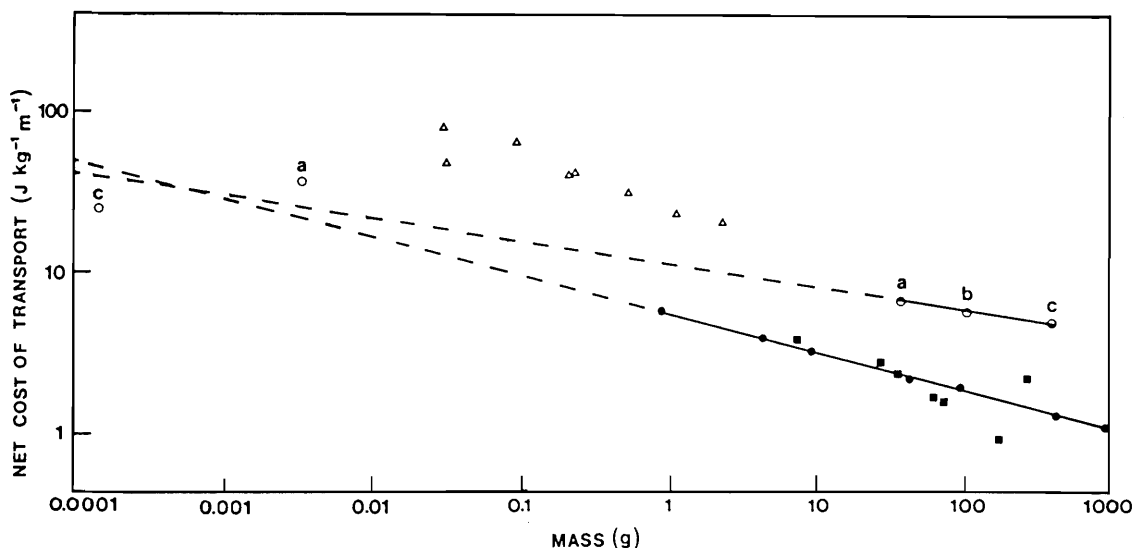


FIG. 1. A comparison of the effect of size on the cost of transport for fish, squid, and crustaceans. Data for fish (●, *Oncorhynchus nerka*; ■, a variety of other fishes) from Beamish 1978, for crustacean (△) from Torres 1984, for adult squid as in Table 2, and for larval squid from O'Dor et al. 1985. Squid (○) species are indicated by letter: (a) *Loligo opalescens*, (b) *Loligo pealei*, and (c) *Illex illecebrosus*.

during active refilling of the mantle (Gosline et al. 1983; Packard and Trueman 1974; Ward 1972), and the elastic energy storage during mantle contraction (Gosline and Shadwick 1983b). The medusae model cannot be applied directly to squid because the jet aperture is directly related to the bell volume in medusae, while funnel aperture in squid changes allometrically. Daniel (1984) suggests that the acceleration reaction may be less important in squid than in many other unsteady swimmers because of their relatively high velocity, but this would also vary with size. The situation in small squids is particularly complex because they routinely move through the range of Reynolds numbers from viscosity-dominated to inertia-dominated situations where there is no adequate expression for estimating drag (Blake 1983). Even the smallest squid hatchlings (150 μg , 2 mm total length) can reach speeds approaching 15 cm s^{-1} during an escape (O'Dor et al. 1985). In addition to these fundamental problems, description of squid locomotion is made more complex by the fact that the fins contribute a proportion of the thrust, which varies from species to species, with size in the same species and with speed in the same animal. As well, squid are divided between negatively buoyant (and generally most active) types, which must work to stay in the water column, and the ammoniacal types, which maintain neutral buoyancy by retaining ammonium in fluid compartments within their tissues (Clarke et al. 1985, 1979; Lipinski and Turoboyski 1983). Neutrally buoyant squid in the water column would presumably have metabolic rates nearly as low as those of the squid in Table 2 at rest on the bottom.

Migrations

If big squids are so inefficient, why are there any at all? There are, in fact, relatively few; of the 176 species of oegopsid squids reviewed by Clarke (1966), only 30% have adults with mantle lengths greater than 15 cm, and nearly all of the large squids are oegopsids. The larger ones are, of course, better known because they are noticeable and of commercial interest. Many of these larger squids are associated with current systems that carry the juveniles to prime feeding sites, and it appears that it is the role of the adults to ensure that eggs are spawned at sites and times that allow the hatchlings to take maximum advantage of patchy

or seasonal resources. In the competition between squid and fish searching for food, relative locomotor efficiency at a particular size may be all that matters, but the spawning adults must cover large distances on fairly rigid schedules. Larger squid travel more efficiently in absolute terms and can cover more distance to be at the right place at the right time. There is even some basis to suggest that large current systems select for large squids (Coelho 1985; Harden Jones 1980).

At the other end of the scale, small eggs may have an advantage for squid that live in the open ocean or in association with current systems beyond increased numbers of offspring. Most cephalopod eggs develop best at higher temperatures (above 15°C) (Boyle 1983) and many are unable to develop at low temperatures (below 10°C) (O'Dor and Balch 1985; Boletzky and Hanlon 1983). Since the depths of nearly all the world's oceans are in the latter category, squid that live above them must avoid having their eggs sink. At low Reynolds numbers small objects fall slower than large ones and upwelling currents would be more likely to keep small eggs above the critical temperature until they had hatched. Squids coat individual eggs with low-density gel to keep them in suspension (Young 1986) or embed their eggs in large masses of gel (O'Dor and Balch 1985; Clarke 1966), but none appear to be able to add lipid to produce flotation as is common in fish (Breder and Rosen 1966), perhaps because of the limitations on lipid metabolism discussed below.

Physiological limitations

The information on locomotion indicates that their molluscan heritage provided squid with a functional system with many good features but inherently less efficient than that of their competitors. Perhaps largely due to the difficulties in maintaining and handling squid (Summers and McMahon 1974; Matsumoto 1976; O'Dor et al. 1977), most aspects of their physiology are less well known than those of fish. The study of neural transmission is a notable exception because intact animals are not required. However, all of the reports cited above also discuss advances in maintenance, and now squid can even be kept in closed culture (Yang et al. 1983; see also Boletzky and Hanlon 1983). Recent studies show that physiological

systems in many squid equal or out-perform those in fish. Following the theme developed above, the comparisons will start with the neuromuscular system.

Most existing literature (Gosline et al. 1983; Packard and Trueman 1974; Wilson 1960) emphasizes the giant fiber system, which controls escape jets in an all-or-none fashion, and discusses a secondary system of slow fibers, which control less dramatic "respiratory" contractions that are also said to produce slow swimming. The general impression is that squid swim in two "gaits," slow and all-out. To date, all such studies have been on restrained animals and are in conflict with all swim-tunnel studies (cited in Table 2) which report that squid can swim reasonably steadily over the full range of sustainable speeds. Available data (Webber and O'Dor 1986) also indicate that this is achieved by graded changes in both frequency of contraction and peak pressure. The results from the two types of studies are clearly in conflict, and neurophysiological studies of free-swimming squid are required to fully appreciate the complexity of the system controlling jet propulsion. The question of the integration of the jet system with fin action, which may provide additional forward thrust during mantle refilling, is virtually unexplored. A potential for rapid advances in this area exists because the work done by squid during jet-propulsion can be directly measured by monitoring the pressure in the mantle cavity, allowing the separate contribution of the fins to be evaluated. The swimming dynamics of free-swimming squid appear to be much more amenable to study than those of undulatory fish, since mantle cavity pressure can be measured using ultrasonically transmitting transducers carried inside the mantle (Webber and O'Dor 1985, 1986).

The mechanical organization of squid mantle has recently been reviewed (Gosline and DeMont 1985) and illustrates the degree of sophistication required by these invertebrates to make their "reciprocating engines" compete with the "turbines" of fish. The main power for the jet comes from the contraction of the circular muscles, which are helically striated to allow isotonic contraction over the greatest possible range of lengths (Gonzalez-Santander and Socastro Garcia-Blanco 1972; Kier 1985). As they become maximally contracted, the decreasing diameter of the mantle means that they continue to work while pumping less and less water. To avoid wasting the output of the muscles during this period, part of the energy is stored elastically in triangular arrays of collagen fibers (Gosline and Shadwick 1983b). As the muscles relax, this stored energy reexpands the mantle, producing negative pressures that draw water in to refill it. A high proportion of the mantle musculature consists of radial fibers that thin the mantle as they contract. The exact proportion varies with species and in general the most active swimmers have more. The central layer of radial fibers are predominantly anaerobic and are analogous with the white muscle in fish, both biochemically (Mömmensen et al. 1981; Bone et al. 1981) and in the sense that they are used primarily in escape or pursuit. When the radial muscles contract, they actively refill the mantle cavity, stretching the circular muscles and giving them a larger volume of water to work against (Ward 1972; Ward and Wainwright 1972). This could potentially increase thrust and (or) Froude efficiency. The picture is even more complex, however, since Gosline et al. (1983) also observed jet cycles in which only the radial muscles contracted, suggesting that squid can use either a cycle from maximum diameter (radials contracted) to resting diameter (radials relaxed) or from resting diameter (circulars relaxed) to minimum diameter (circulars contracted). This is analogous to a horse

changing from a trot to a canter to rest one set of muscles and, continuing the analogy, to a gallop to use more muscle. During maximal effort both sets of muscles are used by squid to maximize the volume of water pumped.

Swimming at their maximum sustainable speeds, squids consume more oxygen per unit weight than similar-sized fish at equivalent temperatures, indicating that their respiratory and circulatory systems have greater capacities. There are few studies on the most active cephalopods, but considerable data on *Octopus* and *Sepia* provide at least an indication of what can be expected. Surprisingly, the anatomical fact that these two species (and presumably the more demanding squids) have their gills arranged to take advantage of the efficiencies of counter-current exchange, like fish, was only recognized in 1982 (Wells and Wells). Typical measured values for extraction are given in Table 3, but they noted that hyperventilation is a common response to stress in cephalopods and recorded extractions as high as 76% in *Octopus* and 68% in *Sepia*. This process produces arterial blood saturation normally in excess of 98% and even in waters with PO_2 below 2.5 kPa saturation never drops below 70% (Houlihan et al. 1982). These excellent loading characteristics have been attributed to the large Bohr coefficients (Brix et al. 1981), which, in the absence of lactic acid secretion (see Changing gears below), may have little effect on oxygen unloading at the tissues. Houlihan et al. (1982) have argued that there are significant effects in both sites. Lykkeboe and Johansen (1982) give additional coefficients, including two squid, *Nototodarus sloani* at -1.16 and *Sepioteuthis lessoniana* at -1.09 , and suggest a relation between the coefficient and the ability to adapt to anaerobic conditions. In some cases the pigment hemocyanin seems to be so carefully "tuned" to deliver oxygen under particular conditions that even a relatively small change in temperature can be lethal (Brix 1983). More data, particularly on the arteriovenous differences in pH and PCO_2 in active squid are needed before the full role of this very adaptable respiratory pigment can be understood.

Unloading of oxygen is very efficient in the coleoids with 85+% removal even in resting animals, and for *Loligo* this much oxygen can be delivered to tissues at relatively high PO_2 's, over 6.5 kPa. Efficient release is critical, since the oxygen carrying capacity of cephalopod blood is, at best, less than half that of fish, presumably because two of the copper-bearing hemocyanin monomers are required to bind one O_2 and because, even in 2 000 000+ dalton complexes, soluble proteins produce higher viscosities and cannot be carried in concentrations as high as cell-bound proteins (Bonaventura and Bonaventura 1983). Thus, even with this high efficiency, squid only equal fish, and they have little margin to increase delivery during exercise.

It appears that the only way a squid can meet its resting oxygen demand, let alone its maximum demand, is by pumping large volumes of blood. With a delivery of 3.8 mL O_2 /100 mL blood, a cardiac output of 132 mL $kg^{-1}min^{-1}$ would be needed to meet the resting requirement of 5 mL $O_2 kg^{-1}min^{-1}$ and 419 mL $kg^{-1}min^{-1}$ to meet the active rate. Bourne (1982) records quiescent heart rates of 102 min^{-1} for a 100-g *Loligo*, which would mean a stroke volume of 0.13 mL at rest. For *Octopus*, heart rate increases by only about one-third during exercise (Wells 1983); assuming the same change, the maximum stroke volume for *Loligo* would need to be 0.31 mL during maximal exercise. Both rate and volume figures are about double those for *Octopus* (Wells 1983). To deliver the resting volume *Loligo* uses pressures nearly double those of octopus and

TABLE 3. Respiratory and circulatory performance of cephalopods and fish

	<i>Nautilus pompilius</i> ^a	<i>Octopus vulgaris</i> ^b	<i>Sepia officinalis</i> ^c	<i>Loligo pealei</i> ^d	<i>Salmo gairdneri</i> ^e
Temperature (°C)	17	22	22	22	10
Approximate weight (g)	500	1000	300	100	1200
Ventilation volume (mL kg ⁻¹ min ⁻¹)	296	280*	770*	—	200
Oxygen extraction (% from water)	7	63 ^f	40 ^g	—	33
Oxygen consumption (mL kg ⁻¹ min ⁻¹)					
Rest	0.5 ^h	0.7 ⁱ	1.7 ^k	5.0 ^m	0.6
Active	2.2 ^h	2.5 ^j	4.9 ^l	15.8 ^m	4.3
Blood volume (% body weight)		5 ⁿ			5 ^o
Respiratory pigment (% w/v in blood)		9 ^p			8 ^q
Arterial oxygen (volume %)	2.0	3.4	4.0	4.3	10.4
Bohr coefficient (log P ₅₀ /pH)	-0.2	-1.6	-1.5	-1.8	-0.5 ^q
P ₅₀ O ₂ (kPa at pH 7.4)	2.3	6.0	4.3	8.0	2.0 ^q
Venous oxygen (kPa)	2.7	4.0	—	6.4	4.4
Oxygen extraction (% from blood)	35	85	—	88	32
Cardiac output (mL kg ⁻¹ min ⁻¹)					
Rest	5	42	—	130*	18
Active	—	150*	—	420*	53
Circulation time (s)	—	90	—	—	64
Heart rate (beats/min)	12 ^r	45	40 ^s	102 ^s	38
Systolic pressure (kPa)	3.5 ^r	3.9 ^p	—	7.2 ^s	5.6

NOTE: These values (*) were calculated from other data in the table using the Fick principle. All other data from first reference given for species except as noted: (a) Johansen et al. 1978; (b) Houlihan et al. 1982; (c) Brix et al. 1981; (d) Redfield and Goodkind 1929; (e) Kicenuik and Jones 1977; (f) Hazelhoff 1938; (g) Wells and Wells 1982; (h) Redmond et al. 1978 (minimum, 17°C; maximum, 25°C); (i) Wells et al. 1983a; (j) Wells et al. 1983b; (k) Johansen et al. 1982; (l) Montuori 1913 (maximum value); (m) Freadman et al. 1984 and personal communication; (n) O'Dor and Wells 1985; (o) Stevens 1968; (p) Wells 1983; (q) Weber et al. 1976; (r) Bourne et al. 1978; (s) Bourne 1982.

considerably higher than a fish. Whether squid can increase this higher pressure threefold as *Octopus* does (Wells 1983) is as yet unanswered, but they do have the complex elastic arterial structure necessary (Shadwick and Gosline 1983) and a highly aerobic cardiac myofiber design (Dykens and Mangum 1979), which arose during coleoid evolution (Dykens et al. 1982). The mantle contractions probably aid the three hearts in producing these high rates of blood flow. Bourne (1982) reports vena cava pressure pulses coordinated with respiratory activity, and the negative pressures during mantle refilling should increase venous return. Similarly, pressures up to 50 kPa inside the mantle cavity during the jet cycle would provide a powerful push to blood going to unpressurized areas of the body.

The analysis of *Loligo* can be carried one step further using Trueman's (1980) estimate of maximal mantle stroke volume of 500 mL kg⁻¹ and a maximum frequency of 120 min⁻¹ to give a ventilatory volume of 60 L kg⁻¹ min⁻¹. To supply the required 15.8 mL O₂ kg⁻¹ min⁻¹ (Freadman et al. 1984) from saturated seawater at 22°C and 32 ppt salinity containing 5.1 mL O₂ L⁻¹, the extraction efficiency need only be 5%. The cephalopods may take some consolation from this one feature of the system that does not have to be pushed to the limit, but, as Wells (1983) suggested, the use of an "appallingly inadequate" oxygen-carrying system has forced the cephalopods to take heroic

measures in the complexity of design and control of their circulatory systems. Given that they must pump eight times as much blood to go half as fast as a fish, their inability to keep pace with fish is understandable.

Endocrine systems

A number of putative neurosecretory structures have been reported in cephalopods (Joose and Geraerts 1983), but few have been characterized functionally. Two of the earliest reported bear on the discussion above since they are cardioactive. Although there are a wide range of CNS controls on the cardiovascular system, including cholinergic inhibition of the heart, there is little evidence that any of the neurotransmitters (5-hydroxytryptamine, adrenaline, or noradrenaline) that are excitatory *in vitro* are actually released in the heart or effective in the circulation of intact animals (Wells 1983). Neurosecretory cells in the pharyngo-ophthalmic vein (Boycott and Young 1956) produce compounds that are cardioactive *in vitro* (Froesch and Mangold 1976) but probably only act as local vasoconstrictors *in vivo* (Wells and Mangold 1980). A cluster of similar cells in the anterior vena cava (Alexandrowicz 1964) produces a complex of cardioactive materials that are effective *in vivo* (Wells and Mangold 1980), including peptides immunologically similar to oxytocin/vasopressin, enkephalin, melanotropin,

and FMRFamide (Voight et al. 1983). FMRFamide and glutamate have been shown to be cardioexcitatory *in vivo* in *Octopus* (Wells 1983). This neurohaemal center requires further study before its complete role can be understood, but it does show that cephalopods have functional neuroendocrine systems. Its role appears to be most closely analogous to the adrenal medulla in fishes, but its products suggest a similarity to the neurohypophysis. The apparent simplicity of the cephalopod system may reflect lack of information, the fact that cephalopods have never developed osmoregulatory capacities or a much greater dependence on direct neural control of circulatory dynamics.

The only other extensively studied cephalopod endocrine function is the control of reproduction by the optic glands in a pattern "unique among animals" (Joose and Geraerts 1983). Originally described in *Octopus* (Boycott and Young 1956) and studied by Wells and Wells (1969, 1959), the glands appear to be universal among the coleoids (*Sepia*, Defretin and Richards 1967; *Illex*, Rowe and Idler 1978) but are as yet undescribed in the *Nautilus*. The glands are unique in that they produce secretory granules (Defretin and Richards 1967) but show no obvious changes in the rate of granule production coordinated with their influence on the reproductive system (Froesch and Mangold 1977). Froesch (1979) notes that the stellate cells, which enlarge during maturation, also respond to foreign proteins and suggests that their tubular mitochondria may be producing a steroid. Although it remains unclear what the gonadotropin is, it clearly has a broad spectrum of effects related to reproduction and probably has a similar chemistry in squids and octopuses (Wells 1976).

The other unique aspects of this gonadotropin, which are important in the present context, are the control of its production and the range of its effects. The direct control of the glands is by nerves from the subpedunculate lobe, and when these are cut the glands enlarge and become increasingly orange in color as the animal undergoes a rapid precocious maturation. The natural stimuli inducing maturation vary with the species and with day length, light intensity, fasting, etc., but in no case does manipulation of environmental variables produce a response as dramatic as surgical intervention. The hormone stimulates most aspects of reproductive development in both sexes, including secondary sex organs (Wells and Wells 1977), suppresses somatic growth, appetite, and digestion, and enhances muscle protein breakdown (O'Dor and Wells 1978). The general trend towards senescence under the influence of the optic glands can be reversed in some (Wodinsky 1977) but not all (Van Heukelem 1979) cases by their removal. To date there is no strong evidence for any feedback control of the glands or of the involvement of any other hormone in maturation (Joose and Geraerts 1983).

Again, the cephalopod endocrine control system seems incredibly simple in comparison with the gonado-hypothalamo-adenohypophyseal axis in fish (Peter 1984), which can not only alter the timing of maturation but also ensures recovery of the spawner in most cases, regulates the size of the clutch (Goetz 1984), and can even change the sex of the fish (Chan and Yeung 1984). Given the ability of the cephalopod nervous system to integrate a complex array of environmental variables in regulating the onset of maturation via the optic glands (Froesch and Mangold 1977) and the system's general level of sophistication, it is difficult to imagine that semelparity results from a lack of flexibility in this system. The recent observations that indicate iteroparity in *Nautilus* (Saunders 1984) and limited iteroparity in an octopus (Rodaniche 1984) suggest that the use of

semelparity in most coleoids results from selective advantage rather than constraint. Certainly the molluscan heritage did not constrain the gastropods, which manage to use their endocrine systems to regulate some of the most complex reproductive patterns known (Joose and Geraerts 1983).

A final interesting contrast between cephalopods and fish in relation to endocrine control comes from studies that use hormonal manipulation to enhance growth in fish (Donaldson et al. 1979). Growth hormone, corticosteroids, and insulin have all been used successfully to accelerate somatic growth in fish. The fact that the normal hormonal milieu does not produce maximal growth rates suggests that the endocrine system in fish functions to suppress growth. This may be the consequence of the importance of accumulating large lipid energy stores for the slow multiyear life-style of fish, which requires overwintering reserves. Cephalopods given *ad libitum* access to food appear to maintain indeterminate, exponential growth (Forsythe 1986) until production of the gonadotropin begins to mobilize protein reserves from muscle to provide material for gametogenesis (O'Dor and Wells 1978). This lack of control of anabolic processes may also carry over into catabolism in squid. There is reasonable evidence that octopods scale their metabolic rates (M) in the commonly seen pattern where $M = aW^{0.75}$ (Maginniss and Wells 1969), but for squid there is little evidence for this; in fact, the limited evidence available suggests that their weight-specific metabolic rates may be constant over a wide range of body weights (W) (O'Dor and Wells 1986). Whatever the normal cause of metabolic rate scaling—there is no universally accepted explanation—the squid may have abandoned it in their head-long drive to provide more energy for their competition with fish.

Biochemical limitations

Digestion

The diet, digestion, energy reserves, and metabolic pathways of cephalopods also all show common features that set them apart from fish. The most distinctive feature is universal carnivory (see Boyle 1983), which might be viewed as either the cause or the result of these biochemical limitations. Briefly, cephalopods tend to consume high protein diets in large quantities, digest them quickly, have high conversion efficiencies, and grow rather than lay down energy stores. They have metabolisms geared to the immediate use of carbohydrates but capable of operating efficiently on protein reserves. Generally, crustaceans and molluscs (including cephalopods) constitute a larger proportion of the squid's diets than do fish (Boyle 1983).

The digestive systems of cephalopods reflect their molluscan heritage. Rather than passing through a continuous expandable tube, food must be chopped into small particles by the beak and radula before it travels *through* the brain and down the esophagus. Arriving at a nexus, analogous to (and perhaps homologous with) the sorting areas in bivalve guts, lumps of food are sent to the stomach and fluid, with fine suspended particles, is sent to either the caecum or the digestive gland. The details of the digestive process vary with species, but in most the digestive gland processes part of the food intracellularly as is common in other molluscs, with the added feature that the contents of still active digestive vacuoles (boules) are released into the same ducts that bring particles in. The flow in the ducts later reverses and the released enzymes apparently have a major role in the extracellular digestion which, along with the mechanical action of the stomach, breaks down the large lumps. Absorption from the fluid phase occurs predominantly in the caecum, and, when all the digestible material has been removed

from the stomach contents, the residue passes directly into the intestine, which appears to have only a minor role as an absorptive site, being primarily a holding area (Boucher-Rodoni et al. 1986). This design allows meals in different stages of digestion to be processed simultaneously and apparently permits faster processing under comparable conditions than the in-line system of fish (Karpov and Cailliet 1978).

There are no well-controlled studies of nutritional requirements in cephalopods, largely because they prefer live food and suitable artificial diets have not been developed. However, Hirtle et al. (1981) found that the squid, *Illex illecebrosus*, grew more efficiently on crustaceans than fish. This was particularly true when the food fish had a high oil content, which led to the production of oily, floating feces. O'Dor et al. (1984) found a similar situation in *Octopus vulgaris* and also showed, using radioactive tracers, that even for a low-lipid crab meal the absorption efficiency for lipid (45–75%) was much lower than that for protein and carbohydrate (95+%). Vonk (1962) found no emulsifiers in *Octopus*, and the major site of lipid uptake is the digestive gland (O'Dor et al. 1984). This gland also has the only important lipid reserve; cephalopod muscle, for example, has a small percentage of membrane lipids, but no significant lipid storage (Suryanarayanan and Alexander 1971). Taken together, these observations suggest that the ability of cephalopods to digest lipids is limited. Lipids are probably taken up directly by phagocytosis in the digestive gland and remain there until they are mobilized for energy or gonad development.

Energy reserves

A typical squid is about 80% muscle, containing 1–1.5% lipid, and 10% digestive gland (Takahashi 1965). In *Todarodes pacificus* the digestive gland may contain up to 40% lipid and the rest of the viscera (averaging about 5% body weight, including the gonad) up to 20%, giving a maximum total lipid content of about 6% of body weight (Takahashi 1960). A few squid (e.g., *Gonatus fabricii*; Clarke et al. 1979, 1985) that use digestive gland lipids for buoyancy may contain more, but values less than 5% are common. In healthy, growing laboratory octopuses, digestive gland lipids account for only 0.3% of body weight. Based on the metabolic rates in Table 3, an oxy-caloric conversion of 4.6 kcal L⁻¹ O₂ and 9 kcal g⁻¹ lipid, the lipid reserves in squid would last 13 days at rest and only 4 days at full activity. O'Dor et al. (1984) estimated that the lipid reserves in an octopus would last only 1 day at rest if they were the only energy source. In fact, based on tracer studies, they suggested that at the onset of a fast both lipid and protein were mobilized rapidly. The rate of ¹⁴CO₂ production from lipid precursors began to decrease after 4 to 5 days while ¹⁴CO₂ from protein precursors continued to increase. A high proportion of labelled carbohydrate in the diet appeared as ¹⁴CO₂ during the 1st day, but a portion went into a reserve in muscle that was not mobilized during fasting but only during exercise. These observations suggest that *O. vulgaris*, and perhaps cephalopods in general, normally fuel resting metabolism with dietary carbohydrate and amino acids and conserve as much lipid as they can digest. During fasting they switch to amino acids from protein degradation and a limited mix of lipid. Their small glycogen stores (Storey and Storey 1979) are reserved for burst activity. Since the lipid to protein ratio in squid is about 0.15 (Giese 1969), the energy available from protein can be estimated at about twice that from lipid, assuming that, like octopuses, they can mobilize 50% of their body protein and using an energy equivalent of 4.7 kcal g⁻¹ protein.

By comparison, formulated feeds for fish contain 10 to 20% dry weight of lipids, which are handled quite efficiently (Cowey and Sargent 1979), and a 5% reserve of lipids is minimal. Fishes such as pilchards and herring contain up to 25% of their weight in lipids, primarily stored in muscle. The sharks and gadoids have less total lipid (ca. 15%), but their livers may contain up to 80% lipid (Bailey 1952). A well-fed herring could survive over 600 days on lipid alone at the resting rate for a fish given in Table 3, and, even swimming at critical speed, its reserves would last nearly 80 days. Fasting fish, like most other vertebrates, tend to mobilize lipid first and only degrade protein as a last resort (Driedzic and Hochachka 1978; Mommsen et al. 1980).

The mobilization of reserves on long migrations appears to be particularly precarious for squid. From Fig. 1 the cost of transport near optimal speed can be estimated to double the resting metabolic rate of the *T. pacificus* mentioned above, so that lipid would last only 1 week and protein, perhaps, another 2 weeks. However, this squid clearly must feed to fuel spawning migrations of up to 2000 km requiring nearly 11 weeks at speeds averaging 0.3 m s⁻¹, particularly since they are developing gonads at the same time. In fact, O'Dor (1982) estimated that they needed to feed at near their *ad libitum* rates. One possibility is that obligate schooling (Mather and O'Dor 1985; Hurley 1978) provides ample opportunity for intraschool cannibalism, which does occur in squid (O'Dor et al. 1980). Such "social" energy reserves may be a unique solution to the problems of low-efficiency squid with small energy reserves competing with high-efficiency fish with large reserves. Traveling at its optimum speed, the fish above would increase its metabolic rate nearly sixfold but could make the same 2000-km trip in about 5 weeks on 40% of its lipid reserve. The remaining reserves would still allow it to survive several months of fasting and (or) produce a clutch of eggs.

The example above, a clear reminder of the problems energy reserves can overcome, leads to the question, "How did cephalopods come to be so apparently ill-equipped for their competition with fish?" Many molluscs have major carbohydrate reserves; in bivalves glycogen stores as high as 5% of body weight are common (Giese 1969). In cephalopods the highest well-documented glycogen reserves are less than 0.4% of body weight and these are so small, relative to metabolic rate, that a few minutes of activity can significantly deplete them (Storey and Storey 1983). The experiments with octopus suggest that these stores are primarily reserved for bursts of activity, and their main role may be to supply substrate for anaerobic energy production via glycolysis with octopine as the end product (Storey and Storey 1983). It is no more surprising that active coleoid cephalopods should avoid having major energy reserves in glycogen than that bivalves and gastropods should have them, since the energy per unit weight of glycogen with its associated water is only about 10% of that in lipids. For shell-laden, relatively inactive molluscs subject to lengthy periods of anaerobiosis, glycogen is ideal but not for active, shell-less nektonic animals. As was seen with fish, lipid is the preferred store for such animals, and the squid use it more extensively than do other molluscs (Voogt 1983). However, the data given above and studies of lipid metabolizing enzymes (Mommsen and Hochachka 1981; Ballantyne et al. 1981) indicate that their ability to use lipid is limited. It may simply be that the coleoids started with a constraining molluscan heritage and have not yet evolved appropriate enzymes, since their present mode of life probably originated less than 100 million years ago. Or, it may

be that the size of their lipid stores are as large as they can be without upsetting the delicate balance of density required for their swimming style. Fish have dense bones as counterweights, allowing them to carry more lipid than boneless, shell-less coleoids. As a third alternative, perhaps such limitations as these merely set cephalopods on a pathway early in their evolution with alternate optimum tactics as outlined below.

Protein has much to recommend it as an energy reserve in coleoids: (i) For marine animals that produce ammonia as the primary metabolic end product, it has a higher energy yield per unit weight than carbohydrate (4.7 vs. 4.0 kcal g⁻¹; Brett and Groves 1979); (ii) it creates no buoyancy problems; and (iii) when produced in the form of muscle proteins it is an active aid to locomotion rather than an inert hindrance (O'Dor and Wells 1978). A look at the other molluscan classes suggests that ancestral molluscs were well equipped to conserve amino acids since all have high intracellular free amino acid concentrations and some manage to accumulate them against enormous gradients, perhaps even making their living this way (Bishop et al. 1983). Such high intracellular concentrations would presumably make high rates of protein synthesis feasible. Given this background, the first logical step for coleoids requiring higher power outputs to prey on crustaceans or function as nektonic organisms may have been the evolution of enzymes that increased their ability to feed amino acid carbon into the Krebs cycle. The available evidence does indicate that at least critical tissues such as the heart (Hoeger and Mommsen 1985) do make extensive use of some amino acids, and both the tracer studies on octopus (O'Dor et al. 1984) and the emaciated condition of squids at the end of their migrations are consistent with high levels of muscle proteolysis during fasting and exercise. The full picture of how the complete mix of the amino acids produced can be used for energy and the extent to which amino acid catabolism fuels muscle itself is still not available.

Changing gears

A major problem arises in muscle because power consumptions in maximally active muscle cells are among the highest known, while few cells consume less power per unit weight than muscles at rest. Hochachka et al. (1983) compared the mechanisms by which vertebrates and molluscs produce these dramatic shifts. As mentioned earlier, both squid and fish have specialized fibers adapted to work anaerobically for burst activity using glycolysis. Compared with oxidative phosphorylation, which requires mitochondria, glycolysis is a simple pathway based on soluble cytoplasmic enzymes that can be packed in high concentrations into small volumes. This allows more muscle fibrils per unit volume of cell, and the fact that such cells have less need for blood supply means more cells per unit volume of tissue as well (Bone 1978). This system works so well that special isozymes with features optimized for muscle have developed for key enzymes. There are significant differences in muscle metabolism between squid and fish. Squid have less anaerobic capacity (Webber and O'Dor 1985; O'Dor 1982) because their anaerobic end product, octopine, results from the condensation of pyruvate and arginine, which is in limited supply. Although considerable arginine is released when arginine phosphate (the phosphagen squid use instead of creatine phosphate) is used to rephosphorylate ATP during activity, this system is more limited than production of lactate, which fish can simply dump as waste if too much accumulates. The production of octopine is clearly part of the molluscan heritage (Gade 1980), and, while it may be restrictive, it

probably also has essential virtues related to pH stabilization (Zammit 1978).

Apparently isozymes have not developed among the Krebs cycle enzymes of either group, and there are no special tricks for controlling the cycle itself (Hochachka et al. 1983). The only way of increasing Krebs cycle turnover in the aerobic muscle used for sustained activity is to increase enzyme and (or) substrate concentrations. It is clear that squid have higher concentrations of key enzymes such as citrate synthetase than most other molluscs, including the less active coleoids (Baldwin 1982), but for these to work substrate must also be available. The main controls on the Krebs cycle are not within the cycle but rather on the pathways that feed intermediates to it, like the glycolytic pathway. Normally fish fuel the cycle with carbohydrate and (or) fat, and carbon input from both sources is essentially limited at a single point, the addition of acetyl-CoA to oxaloacetate. In the later stages of their migrations salmon switch to protein fuel (Mommsen et al. 1980), which allows five input points to the cycle (Fig. 2). The maximum power output of fish in this condition is apparently unknown, but would be of great interest. The metabolic organization for protein catabolism in squid is certainly different from that in fish, with proline playing a more important role than alanine in the transfer of carbon to nonmuscle tissues (Hoeger and Mommsen 1985), but there is clear evidence for at least one additional entry point in squid (via 2-oxoglutarate, Fig. 3) and others are likely. If squid had to push aerobic metabolism to the limit because of the inefficiency of their propulsion system, perhaps the simplest way was by increasing the concentrations of enzymes for catabolizing the amino acids which were already present in high concentration. Amino acid metabolism may even have been selected for in preference to lipid because of this higher potential power output.

Hochachka et al. (1983) compared the 5- to 20-fold increases in metabolic rate during exercise in vertebrates to the 3-fold increase reported for *Loligo opalescens* (O'Dor 1982) and asked whether the more limited aerobic scope in squid is real or artifactual. The two additional studies of squid in tunnel respirometers (Table 2) appear to confirm that squid, regardless of their life-cycle stage, have maximum metabolic rates much higher than fish but only 3 to 4 times higher than their own resting rates. Similar ratios have also been found in *Octopus* (Wells et al. 1983b). There may be a biochemical basis for this in the pattern of squid metabolism outlined above. The problem lies in the high resting metabolic rates of squid; does the metabolism dictate the life-style or vice versa? Perhaps a system optimized for rapid through-put is less easily shut down; there must be some limit to how efficiently an enzyme can be turned off. If the best ratio of active to standard metabolism vertebrates can achieve when controlling a single entry point is 20:1, one might expect that the best ratio possible with five entry points would be 4:1, since the turnover rate of the cycle would depend on the sum of the inputs. Although oxidation metabolism is normally regulated by ATP energy charge, it would not be surprising to find that the entry point enzymes are unable to suppress their activity completely. It may be more economical to let the system run faster and maintain faster growth and development to use up ATP than to deal with the substrate imbalances that might otherwise develop.

Squid may alleviate this metabolic dilemma to some degree through behaviour. *Illex illecebrosus*, for example, is often found at the surface feeding at night but apparently rests on the bottom at depths as great as several hundred metres during the

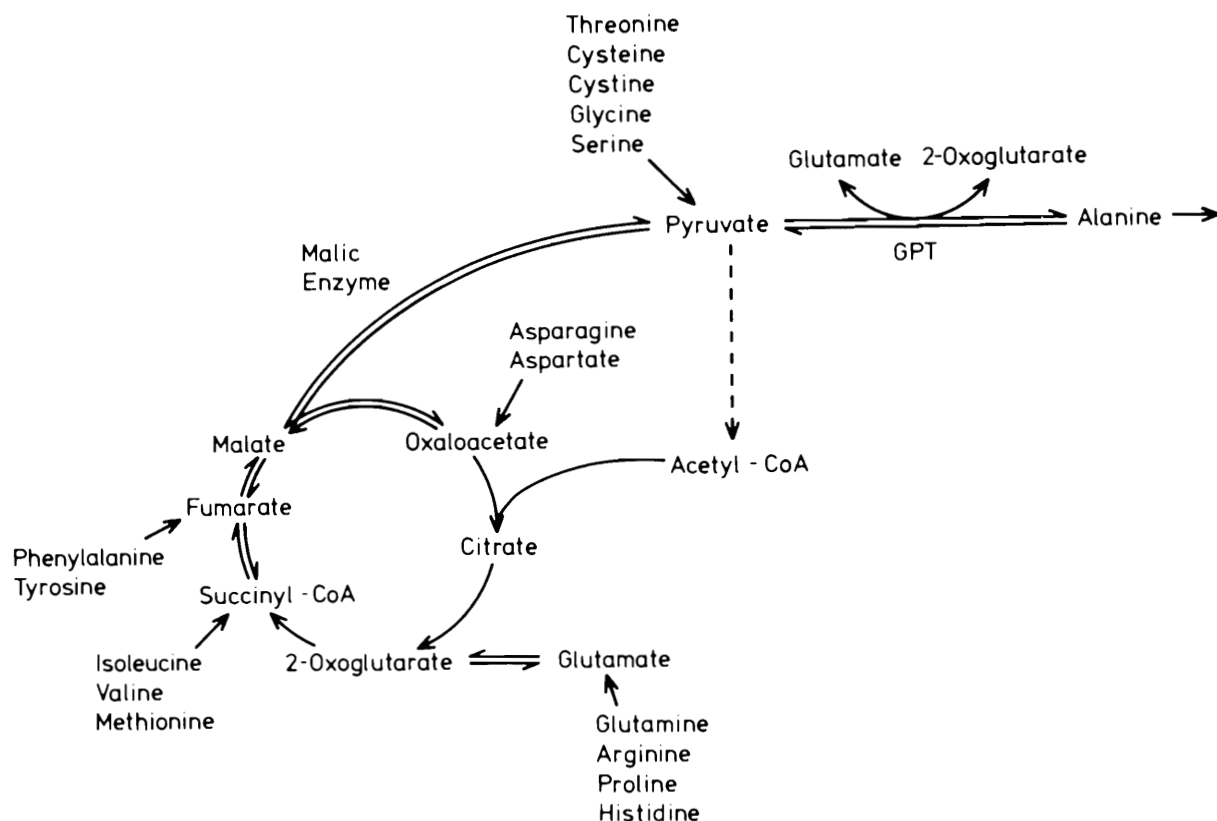


FIG. 2. Proposed organization of amino acid metabolism in salmon white muscle (from Mommsen et al. 1980, with the authors' kind permission).

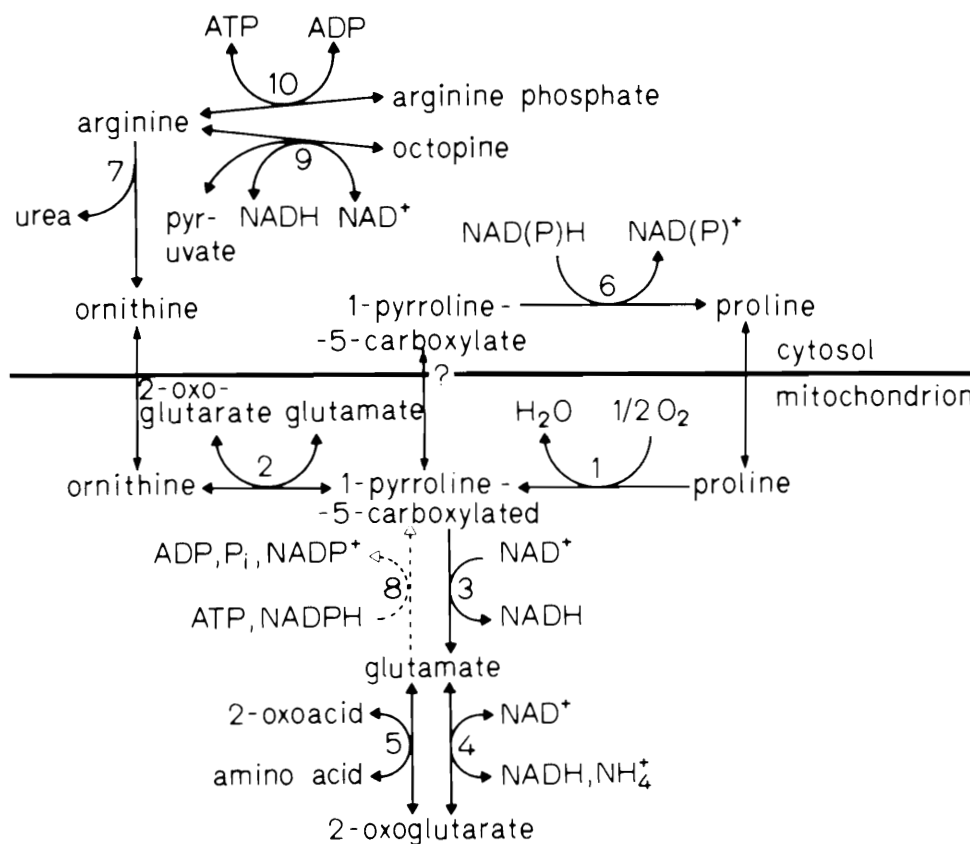


FIG. 3. Identified metabolic pathways for amino acid interconversions in squid heart showing the entry of proline and arginine to the Krebs cycle via 2-oxoglutarate (from Mommsen and Hochachka 1981, with kind permission from the authors and the *European Journal of Biochemistry*).

day. In summer and autumn this exposes it to a temperature differential of about 10°C. DeMont and O'Dor (1984) found dramatic effects of temperature on metabolic rate in this squid, equivalent to a Q_{10} of over 6. This result was based on a regression of data over the season and may have included compounding factors such as developmental changes and paradoxical adaptation (type 5, Precht 1958) seen in preliminary experiments (DeMont 1981); however, even if the short-term Q_{10} is only 2 to 3, this still brings the resting rate of the squid down into the range of a fish at surface temperatures. Most fish could not make such large vertical migrations so quickly or without using considerable energy to refill their swim bladders.

Compensatory complexity

Limited by a molluscan heritage of anatomy, physiology, and biochemistry that doomed them to be second best in all these areas, the cephalopods seem to have been pressed to make adaptations in the one system where they were on an equal footing, nervous control. Packard (1972) pointed out that cephalopods devote a higher proportion of their body weight to the nervous system than any other aquatic poikilotherm and even match the reptiles in this regard. This basic observation has not changed, but there are new developments worthy of review. As already mentioned, the sophistication of the control of the neuromuscular system handling locomotion in squid has been underrated, and neural control of the circulatory system is probably a key to the incredible feats it performs. Recent work shows that, while squid may be more "high strung" and less dexterous than octopods, they are not stupid. Flores (1983) and Allen et al. (1985) have shown that squid have pattern recognition and learning and unlearning curves similar to those of *O. vulgaris* which is at least comparable with fish. Young (1977a) has also added extensively to the literature on the comparative neuroanatomy of cephalopods which provides the necessary basis for understanding both how squid brains work and how they evolved.

Large and complex sections of cephalopod brains are for control of a process fish lack entirely, direct nervous control of color and pattern. Fish chromatophores, controlled hormonally, require minutes to hours to respond and are primarily used for camouflage against a stationary background. Cephalopods can do this too, but also use pattern in other ways and on different time scales (Packard and Hochberg 1977). One of the most common and perhaps oldest uses, which many people have seen to their consternation, is the "disappearing act." When pursued or frightened squid expand their chromatophores to darken and catch the attackers attention, squirt out a squid-shaped blob of ink, contract their chromatophores to become transparent and vanish by using their jet to shoot off in an unexpected direction. Many cephalopods use chromatophore patterns to communicate with conspecifics in mating displays, etc. (e.g., Wells and Wells 1972), and some squid even have controlled light output (Young 1977b). *Sepioteuthis sepioidea* is reportedly able to organize complex social interactions by visual signals, including hunting in packs. Even a pattern-based language has been described (Moynihan and Rodaniche 1982; Moynihan 1985). The degree of social organization in more widely ranging oceanic species remains unclear, but one certainly has the impression that there is more going on than a simple random association of equal individuals as is found in most fish schools.

Conclusions

The competition between squid and fish has obviously been complex and multifaceted, but the picture that emerges from the

observations outlined above suggests that squid are still far from being directly competitive with fish. There are too many things that fish do well that squid either do poorly or cannot do at all. On the other hand, there appear to be some things that squid can do better. The stage seems to have been set for squid to specialize in short life cycles with rapid growth and an emphasis on a large investment in numerous offspring, in contrast to the pattern of fish which typically shows long-lived adults investing only as much in reproduction as they can afford while still ensuring their own survival. Among the factors favoring small squid are (i) the possibility of a more favorable relative locomotor efficiency vis-à-vis both fish and crustaceans, (ii) a body plan and nervous system that increase the probability of prey capture and predator avoidance, (iii) a digestive system capable of handling more through-put of flesh with equal efficiency, and (iv) an amino acid based metabolism that favors rapid growth because it provides both high concentrations of amino acids for protein synthesis and high resting ATP production to fuel the synthetic process. The locomotion of adult squid, however, becomes increasingly inefficient relative to the only prey that are really large enough to make predation worthwhile, fish. Adult squid also lack the capacity to store reserves that would allow them to migrate, breed, and overwinter sequentially. The traits of fish need not be cataloged since they are generally the reverse of those of squid. The tactics of squid allow them to take maximum advantage of intermittent or patchy resources but are likely to produce dramatic annual variations in both numbers and biomass. The tactics of fish allow them to "ride out" lean years, with some sacrifice of biomass producing relative numerical stability.

The view presented here may not be the only one possible, but there seem to be strong arguments (some, admittedly, in need of verification) to suggest that a number of fundamental, energy-related constraints on squid have favored selection for short life histories and semelparity in squid and that their endocrinology has merely reflected rather than caused their differences from fish. Despite the functional similarities created by competition in the nekton, it is tempting to suggest that squid are no longer so much competing with fish as trying to stay out of their way.

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