Interrelationships Between Swimming Speed, Caudal Fin Aspect Ratio and Body Length of Fishes

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Abstract

The aspect ratio of the caudal fin of 63 fish species was measured. Swimming speeds for these species, representing 129 cases, were obtained from the literature for various fish sizes and speeds, i.e., "minimum speed" for sustained swimming and "maximum speed" (+ "burst" speed). Results show a very significant relationship of these two speeds with aspect ratio. The relationship described here allows for reliable estimations of individual speeds of the various species included. It also serves to illustrate the functional dependence of speed on the aspect ratio and length of the fish.

Introduction

The metabolic rate of animals is controlled by factors which are inherent to the organisms themselves, by environmental factors and by interactions between these two set of factors.

In studies concerning growth and production of fish populations, it is particularly important to take account of the bioenergetics of the organisms concerned (see, e.g., Vivekanandan and Pandian 1977 or Ware 1978). However, estimating food consumption in the field is a very tedious undertaking. Palomares and Pauly (1989), based on data in Palomares (1987), proposed an empirical model for obtaining food consumption estimates from the level of activity of the fish, as indicated by the aspect ratio of their caudal fin (A). They observed that fishes with high aspect ratios are active fishes with high metabolic rates of food consumption while fish with low aspect ratios had low metabolism and food consumption.

The Caudal Fin and Its Aspect Ratio

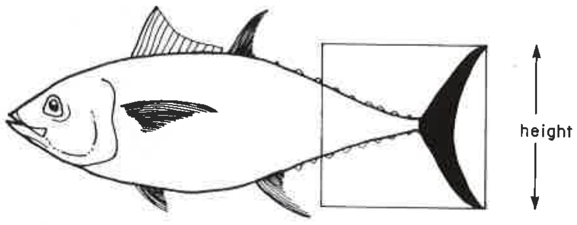
The caudal fin contributes a great deal to the locomotor activities of the fish, particularly in those species which are pelagic and relatively short-bodied. The mechanics of caudal fin swimming have been described in several works, e.g., Gray (1971), Nursall (1979), Alexander (1967), Webb (1975, 1982, 1984) for general descriptions; Budker (1971), Webb and Keyes (1982) for sharks; and Magnuson and Prescott (1966) and Magnuson (1970, 1973, 1978) for scombroid and xiphoid fishes.

A swimming fish acts upon two opposing forces as it propels its body forwards - the lift and the drag. The ratio between these two forces determines the effort required for movement, i.e., the greater the lift-drag ratio the lesser the energy requirement. This ratio is highest when the *aspect ratio* (A) of the caudal fin (Fig. 1) is high (Alexander 1967). A is defined by

$$A = h^2/s \qquad \text{...1)}$$

where h pertains to the span or height of the caudal fin and s is its surface area.

A. *Thunnus obesus*, A = 7.48



B. *Pomatochistus minutus*, A = 0.60

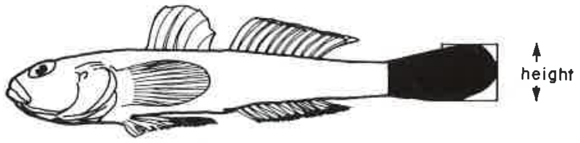


Fig. 1. Aspect ratio ($A = h^2/s$, h = height of the caudal fin; s = surface area of fin) of a pelagic fish (A) and a bottom dweller (B). Note the correspondence between aspect ratios and modes of life. Measurements of the surface area of the caudal fin use the narrowest portion of the caudal peduncle as cutoff limit. (This differs slightly from the cutoff limit used in Palomares and Pauly (1989) and Pauly (1990), but allows for better reproducibility of A values.)

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High aspect ratio has been widely discussed as a contributor to the rapid swimming of pelagic fishes (Magnuson and Prescott 1966; Alexander 1967; Budker 1971), but a relationship directly linking A to speed appears to be currently unavailable.

Materials and Methods

Swimming speeds for all the fishes included here were taken from literature sources. The lengths of the fishes for which swimming information was available were noted and standardized to standard length (SL in cm). Swimming modes were given as (i) "minimum" or "sustained" or "cruising" speeds which for the purpose of this contribution were attributed the value "0" and (ii) "maximum" or "burst" speeds, given the value "1". The values "0" and "1" were then used as dummy variables in a multiple linear regression analysis. Speeds were expressed in absolute (km hour^{-1}) and relative terms (body length second^{-1}).

Temperatures (°C) typical for each fish were noted along with the body depth ratios (D), i.e., length/maximum body depth.

The aspect ratios were measured using enlarged pictures of the fishes, following Fig. 1 and equation (1). Caudal fin heights, including fishes with heterocercal fins, were measured by projecting a line along the horizontal axis of the fish body and taking measurement at right angles with the body.

Results and Discussion

Table 1 lists the species considered here, in systematic order, the corresponding measurements and their references.

A wide range of fish sizes were covered, i.e., from goby, *Pomatochistus minutus* (7.0 cm SL) to basking shark, *Cetorhinus maximus* (700 cm SL). The goby had the lowest A value: 0.60. Among the species/groups with high values of A were the scombrids, ranging

Table 1. List of species and variables used in the multiple linear regressions.

Species	Family	L (SL, cm)	A	M^c	S (l sec^{-1})	Ref. no.^{d}
1 *Ginglymostoma cirratum*	Orectolobidae	193.6^a	0.760	0	0.255	27
2 *Cetorhinus maximus*	Lamnidae	700.0	3.316	1	0.106	12
3 *Cetorhinus maximus*	Lamnidae	700.0^b	3.316	0	0.395	17
4 *Carcharhinus leucas*	Carcharhinidae	152.4	3.851	1	3.461	7, 13
5 *Carcharhinus leucas*	Carcharhinidae	173.5^a	3.851	0	0.752	27
6 *Carcharhinus melanopterus*	Carcharhinidae	75.1^a	2.205	0	1.033	27
7 *Negaprion brevirostris*	Carcharhinidae	177.1^a	1.562	0	0.597	27
8 *Negaprion brevirostris*	Carcharhinidae	184.2	1.562	1	1.310	7, 13
9 *Triakis semifasciata*	Carcharhinidae	79.1^a	0.884	0	0.719	27
10 *Sphyrna tiburo*	Sphyrnidae	70.5^a	1.633	0	1.108	27
11 *Alosa pseudoharengus*	Clupeidae	28.4^b	2.055	1	16.903	22
12 *Brevoortia tyrannus*	Clupeidae	25.0^b	1.885	0	0.512	4, 5
13 *Clupea harengus*	Clupeidae	25.0	1.711	1	6.973	13
14 *Sprattus sprattus*	Clupeidae	12.0	1.805	1	5.215	13
15 *Sprattus sprattus*	Clupeidae	7.6^b	1.805	1	18.350	22
16 *Engraulis mordax*	Engraulidae	3.7^b	2.253	1	8.109	22
17 *Esox lucius*	Esocidae	20.0	2.350	1	7.378	13
18 *Esox lucius*	Esocidae	44.0	2.350	1	6.502	13
19 *Esox lucius*	Esocidae	16.1	2.350	1	13.032	13
20 *Oncorhynchus gorbuscha*	Salmonidae	64.0	2.472	0	0.969	23
21 *Oncorhynchus nerka*	Salmonidae	63.0	2.701	0	0.937	23
22 *Oncorhynchus nerka*	Salmonidae	8.6	2.701	0	3.651	23
23 *Oncorhynchus nerka*	Salmonidae	67.6	2.701	0	0.681	23
24 *Oncorhynchus tshawytscha*	Salmonidae	19.9^b	2.477	1	3.019	18
25 *Oncorhynchus tshawytscha*	Salmonidae	31.5^b	2.477	1	2.250	18
26 *Salmo irideus*	Salmonidae	12.6^b	1.686	1	17.462	22
27 *Salmo irideus*	Salmonidae	29.2	1.686	1	9.952	7
28 *Salmo irideus*	Salmonidae	20.0	1.686	1	8.496	7
29 *Salmo trutta*	Salmonidae	38.0	1.206	1	8.588	13
30 *Salmo trutta*	Salmonidae	24.0	1.206	1	9.873	13
31 *Abramis brama*	Cyprinidae	24.0	1.728	1	4.097	13
32 *Carassius auratus*	Cyprinidae	7.0	1.477	1	9.607	7
33 *Carassius auratus*	Cyprinidae	13.0	1.477	1	13.053	7
34 *Carassius auratus*	Cyprinidae	12.5	1.477	1	12.873	13
35 *Chalcalburnus chalcoides*	Cyprinidae	12.3^b	2.139	1	15.448	22
36 *Cyprinus carpio*	Cyprinidae	13.5	2.176	1	12.582	13
37 *Leuciscus leuciscus*	Cyprinidae	9.2	1.286	1	17.542	7
38 *Leuciscus leuciscus*	Cyprinidae	20.0	1.286	1	12.297	7
39 *Leuciscus leuciscus*	Cyprinidae	18.1	1.286	1	9.383	7
40 *Leuciscus rutilus*	Cyprinidae	24.0	1.686	1	5.215	13
41 *Scardinius erythropthalmus*	Cyprinidae	24.0	2.353	1	7.263	13
42 *Scardinius erythropthalmus*	Cyprinidae	22.0	2.353	1	5.892	7
43 *Scardinius erythropthalmus*	Cyprinidae	22.3	2.353	1	5.827	7
44 *Gadus morhua callarius*	Gadidae	56.0	0.768	1	3.831	13
45 *Melanogrammus aeglefinus*	Gadidae	9.5^b	1.325	1	27.371	22
46 *Melanogrammus aeglefinus*	Gadidae	42.0	1.325	1	4.363	13
47 *Merlangius merlangus*	Gadidae	20.0	0.903	1	8.046	13

Continued

Table 1. Continued

Species	Family	L (SL, cm)	A	M[c]	S (l sec^{-1})	Ref. no.[d]
48 *Merlangius merlangus*	Gadidae	15.2	0.903	1	9.869	22
49 *Pollachius virens*	Gadidae	21.0	1.296	1	9.578	13
50 *Pollachius virens*	Gadidae	37.5	1.296	0	3.400	20
51 *Pollachius virens*	Gadidae	43.1[b]	1.296	1	6.961	22
52 *Spinachia spinachia*	Gasterosteidae	10.0	0.852	1	7.152	13
53 *Sebastes mystinus*	Scorpaenidae	15.1	1.600	1	7.020	3
54 *Sebastes mystinus*	Scorpaenidae	15.1	1.600	0	3.643	3
55 *Sebastes serranoides*	Scorpaenidae	19.8	1.369	0	2.677	3
56 *Morone sexatilis*	Percichthyidae	22.8[a]	2.309	0	1.884	6
57 *Lucioperca sandra*	Percidae	44.0	1.329	1	4.368	13
58 *Perca fluviatilis*	Percidae	24.0	1.480	1	5.401	13
59 *Pomatomus saltatrix*	Pomatomidae	22.6[a]	2.547	0	1.836	6
60 *Trachurus mediterraneus*	Carangidae	16.0[b]	3.656	1	17.501	22
61 *Trachurus symmetricus*	Carangidae	6.7[b]	4.288	1	14.180	22
62 *Coryphaena hippurus*	Coryphaenidae	67.2[b]	1.205	0	0.845	8
63 *Leiostomus xanthurus*	Sciaenidae	5.0	1.388	1	14.001	22
64 *Cymatogaster aggregata*	Embiotocidae	9.3	2.269	1	11.614	3
65 *Cymatogaster aggregata*	Embiotocidae	9.3	2.269	0	4.947	3
66 *Embiotoca jacksoni*	Embiotocidae	14.9	1.828	0	3.490	3
67 *Embiotoca jacksoni*	Embiotocidae	14.9	1.828	1	7.517	3
68 *Hyperprosopon argenteum*	Embiotocidae	13.7	2.450	0	3.066	3
69 *Hypsurus caryi*	Embiotocidae	13.8	2.408	0	3.044	3
70 *Phanerodon furcatus*	Embiotocidae	15.5	1.707	0	3.097	3
71 *Chromis punctipinnis*	Pomacentridae	8.5	1.573	1	11.060	3
72 *Chromis punctipinnis*	Pomacentridae	8.5	1.573	0	6.000	3
73 *Mugil auratus*	Mugilidae	21.9[b]	1.325	1	20.550	22
74 *Mugil cephalus*	Mugilidae	3.5[b]	2.549	1	20.002	22
75 *Mugil saliens*	Mugilidae	17.9[b]	1.556	1	22.348	22
76 *Sphyraena barracuda*	Sphyraenidae	129.5	2.556	1	9.526	10
77 *Pomatochistus minutus*	Gobiidae	7.0	0.600	1	3.831	13
78 *Acanthocybium solandri*	Scombridae	125.0[b]	6.422	0	0.328	10
79 *Acanthocybium solandri*	Scombridae	89.8[a]	6.422	1	13.383	10
80 *Acanthocybium solandri*	Scombridae	110.2[a]	6.422	1	19.361	10
81 *Acanthocybium solandri*	Scombridae	97.6[a]	6.422	1	12.415	10
82 *Auxis rochei*	Scombridae	31.0[a]	6.669	0	2.194	10
83 *Euthynnus affinis*	Scombridae	36.0	5.611	0	2.111	10
84 *Euthynnus affinis*	Scombridae	40.0	5.611	1	10.001	10
85 *Euthynnus affinis*	Scombridae	40.0	5.611	1	12.501	10
86 *Katsuwonus pelamis*	Scombridae	48.4[a]	6.969	1	19.630	10
87 *Katsuwonus pelamis*	Scombridae	48.0	6.969	0	1.500	10
88 *Katsuwonus pelamis*	Scombridae	38.0	6.969	0	1.553	10
89 *Katsuwonus pelamis*	Scombridae	79.0	6.969	1	8.051	10
90 *Katsuwonus pelamis*	Scombridae	64.0	6.969	1	8.782	10
91 *Katsuwonus pelamis*	Scombridae	44.0	6.969	0	1.500	10
92 *Katsuwonus pelamis*	Scombridae	44.0	6.969	0	1.727	10
93 *Katsuwonus pelamis*	Scombridae	48.0	6.969	1	14.334	10
94 *Katsuwonus pelamis*	Scombridae	57.0	6.969	1	10.317	10
95 *Katsuwonus pelamis*	Scombridae	48.4[a]	6.969	1	15.497	10
96 *Katsuwonus pelamis*	Scombridae	39.0	6.969	0	2.154	10
97 *Sarda chiliensis*	Scombridae	57.0	3.706	1	6.492	10
98 *Sarda chiliensis*	Scombridae	57.0	3.706	0	1.544	10
99 *Sarda sarda*	Scombridae	16.0	4.538	0	2.188	10
100 *Sarda sarda*	Scombridae	14.9[a]	4.538	1	8.586	10
101 *Scomber japonicus*	Scombridae	34.2	5.157	0	2.709	19
102 *Scomber japonicus*	Scombridae	27.1[a]	5.157	1	8.356	22
103 *Scomber scombrus*	Scombridae	33.4[a]	4.008	1	8.983	13
104 *Scomber scombrus*	Scombridae	32.0	4.008	0	0.875	10
105 *Scomber scombrus*	Scombridae	30.5	4.008	0	3.279	22
106 *Scomber scombrus*	Scombridae	38.0	4.008	1	7.999	13
107 *Scomber scombrus*	Scombridae	30.5	4.008	1	18.034	22
108 *Scomber scombrus*	Scombridae	32.0	4.008	0	6.326	20
109 *Scomber scombrus*	Scombridae	19.0	4.008	0	1.158	10
110 *Thunnus albacares*	Scombridae	66.5	7.212	1	31.089	10
111 *Thunnus albacares*	Scombridae	62.1[a]	7.212	1	15.997	10
112 *Thunnus albacares*	Scombridae	84.0	7.212	0	0.774	10
113 *Thunnus albacares*	Scombridae	62.1[a]	7.212	1	8.409	10
114 *Thunnus albacares*	Scombridae	66.5[a]	7.212	1	18.855	10
115 *Thunnus albacares*	Scombridae	87.0	7.212	0	0.575	10
116 *Thunnus albacares*	Scombridae	52.0	7.212	1	10.482	10
117 *Thunnus albacares*	Scombridae	35.0	7.212	0	1.314	10
118 *Thunnus albacares*	Scombridae	85.0	7.212	0	0.765	10
119 *Thunnus albacares*	Scombridae	62.1[a]	7.212	1	11.083	10
120 *Thunnus obesus*	Scombridae	36.0	7.482	0	1.306	10
121 *Thunnus obesus*	Scombridae	55.0	7.482	0	1.091	10
122 *Thunnus thynnus*	Scombridae	250.0	5.535	0	0.880	10
123 *Thunnus thynnus*	Scombridae	216.0	5.535	0	1.343	10
124 *Thunnus thynnus*	Scombridae	213.0	5.535	0	1.643	10
125 *Thunnus thynnus*	Scombridae	241.0	5.535	0	1.120	10
126 *Thunnus thynnus*	Scombridae	219.0	5.535	0	1.096	10
127 *Thunnus thynnus*	Scombridae	226.0	5.535	0	1.328	10
128 *Xiphias gladius*	Xiphiidae	220.0	5.813	1	11.365	22
129 *Ophiocephalus striatus*	Channidae	3.8	1.300	0	1.548	21

[a] Values originally given as total lengths (TL).
[b] Values originally given as fork lengths (FL).
[c] Swimming mode ("0" for sustained, "1" for burst).
[d] Refer to the list of references.

from 3.71 to 7.48 ($\bar{X} = 6.0$); the swordfish, *Xiphias gladius* with 5.81; carangids, 3.66 to 4.29 ($\bar{X} = 3.97$); *Oncorhynchus* spp., 2.47 to 2.70 ($\bar{X} = 2.58$); and sharks, 0.76 to 3.85 ($\bar{X} = 2.31$).

Swimming speeds varied considerably from species to species. The lowest relative speed occurred in the biggest fish, the basking shark, *Cetorhinus maximus*, with 0.11 l sec^{-1}. Thus, an anchovy *Engraulis mordax* of 3.7 cm could have a relative swimming speed thirty times higher than that of a basking shark. Juvenile *Melanogrammus aeglefinus* (9.5 cm SL) attain relative burst speeds of up to 27.4 l sec^{-1}. Corresponding values for the scombrid family range from 0.58 to 31.1 l sec^{-1}.

The regression analyses were carried out using several variables presumed to be directly related with swimming speed as dependent variable, i.e., body depth ratio, caudal fin aspect ratio, body length, swimming mode and habitat temperature. Two of these variables, (depth ratio and water temperature) were found not to be significantly correlated with swimming speed and were hence disregarded for the final analysis.

The predictive models derived were:

Model 1:

$$\log_{10}(Sa) = -0.828 + 0.6196\log_{10}(L) + 0.3478\log_{10}(A) + 0.7621(M) \qquad ...2)$$

and Model 2:

$$\log_{10}(Sr) = 0.616 - 0.3804\log_{10}(L) + 0.3478\log_{10}(A) + 0.7621(M) \qquad ...3)$$

where Sa and Sr are the absolute (km hour^{-1}) and relative (l sec^{-1}) swimming speeds of the fish, respectively, L is the standard length in cm, A is the aspect ratio and M is the swimming mode ("0" for sustained and "1" for burst speeds).

With R = 0.879, both models explain 77% of the variance of the dataset in Table 1. The standard deviation of the residuals was 0.25 $\log_{10}$ units which corresponds to a factor of 1.78 about the predicted values. Table 2 shows the parameter estimates and related statistics.

Fig. 2 shows the plots of the observed *vs.* predicted values of swimming speed. As shown in the graph, a one-to-one correspondence exists between the X and Y values indicating that reasonable estimates were obtained by the model. A pronounced separation between the sustained and burst swimming values is also observed.

Worth noting is the peculiar behavior of the maximum speeds of the shark *Cetorhinus maximus* whose swimming speed is overestimated by equations (1) and (2). This confirms the finding of Budker (1971) that basking sharks have tails typical of fast-moving sharks but are "slow and sluggish creatures". The aspect ratio calculated

Table 2. Parameter estimates obtained for Models 1 and 2 with related statistics.

Parameters	Model 1 estimates	s.e.	P(t-test)	Model 2 estimates	s.e.	P(t-test)
Coefficient of determination (R^2)	0.77	-	-	0.77	-	-
d.f.	123	-	-	123	-	-
Intercept	-0.8280	0.2299	-	0.6160	0.2299	-
log Length (cm)	0.6196	0.0562	<0.001	-0.3804	0.0562	<0.001
log Aspect ratio	0.3478	0.0782	<0.001	0.3478	0.0782	<0.001
Swimming mode	0.7621	0.0435	<0.001	0.7621	0.0435	<0.001

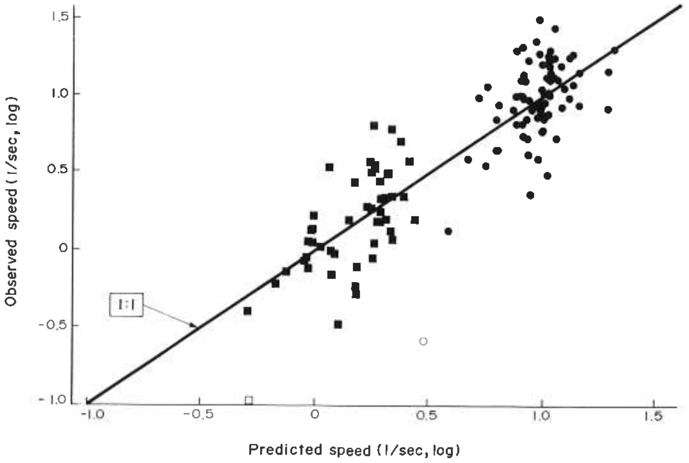

Fig. 2. Observed versus predicted relative swimming speeds (l sec^{-1}) for 63 fish species (R = 0.88). Minimum speed (closed squares); maximum speed (closed dots); minimum speed of *C. maximus* (open square); maximum speed of *C. maximus* (open dot). The diagonal identity line (1:1) is provided for reference.

for this species (3.36) was comparable to those of the *Carcharhinus* spp. ($\overline{X}$ = 3.302), which are fast-swimming sharks. This explains why the model overestimates the speed of *C. maximus*. Other shark estimates, however, conformed well with the observed values.

To further illustrate the dependence of the swimming activities of fish with A and body size, swimming speeds for different sizes of *Pomatochistus minutus* and *Thunnus obesus* are plotted in Fig. 3. For purposes of comparison, similar length scales were used for both fishes.

In summary, the empirical models presented in this contribution may well be used for the estimation of the swimming speeds (or perhaps activity levels as related to metabolic rates) in fishes. Some limitations with regard to the use of these models are identified: (i) the models can only be used to predict speeds for fishes using the caudal fin as the major locomotory organ; and (ii) over- or underestimation of S may occur in some fishes with aberrant behavior, as was here the case with basking shark.

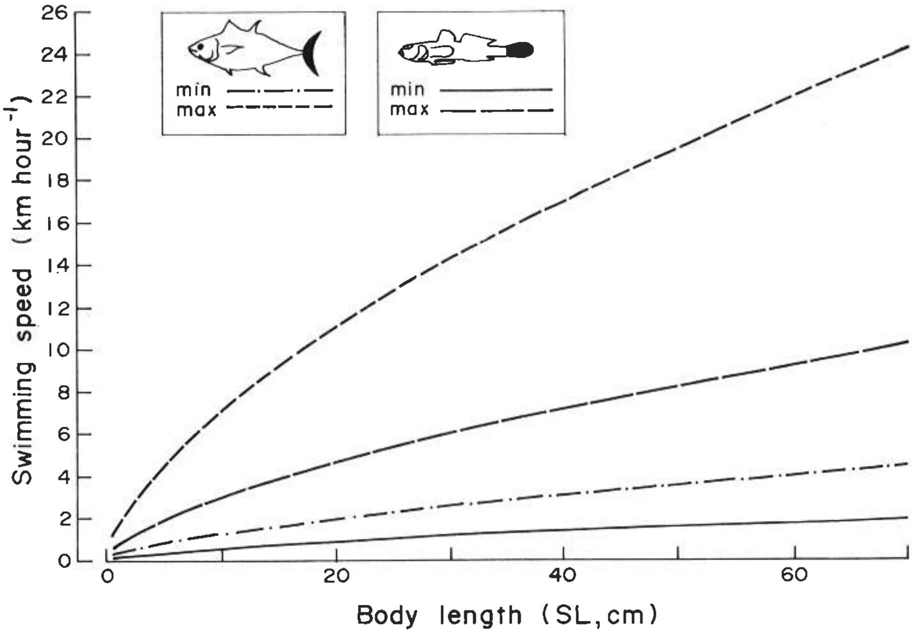

Fig. 3. Relationship between swimming speed (km hour^{-1}) and the body length of fishes with different aspect ratios (see Fig. 1).

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