

Pelagic food webs in the tropical Pacific

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Abstract

Analysis of stomach contents, feeding rhythms, vertical distributions, and day-night migrations of the successive links of a pelagic food chain leads to a functional model of the prevailing trophic relationships and to identification of basic mechanisms determining the food web structure. This model demonstrates the existence of processes which support the downward energy transfer and reduce the upward one.

A comparative analysis of the food of longline tuna and the food of the fish they prey upon, and also of their bathymetric distribution and that of the fauna upon which they feed, led to a proposal in earlier publications (Legand et al. 1972; Roger 1973, 1974a) of a pattern of trophic relationships in the tropical Pacific. More abundant material has now been analyzed which improves the reliability and precision of the structures described: we have 365 analyses of stomach contents of albacore [*Thunnus (Germo) alalunga*] and yellowfin tuna [*Thunnus (Neothunnus) albacares*] as against the previous figure of 156. Roger (1975) has also completed a study of the feeding patterns of certain prey (euphausiids) consumed by the fish that the tuna eat.

It is now possible to give a scheme which covers the whole chain: phytoplankton, small zooplankton → euphausiids → micronektonic fishes → longline tunas. This chain is important among the food webs upon which the longline tunas rely as micronektonic fishes account for 60% of their diet by volume, the remaining 40% being mainly cephalopods (Legand et al. 1972). It can be assumed that longline tunas themselves make up a notable part of the large nekton of these regions, despite the lack of information on the relative biomass of the different species of pelagic predators (tunas, marlins, sharks, etc.).

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Material and methods

The stomach contents of 365 albacore and yellowfin tunas caught by longlining have been analyzed and 1,399 micronektonic fishes therein identified (Legand et al. 1972). The stomachs of 667 of the latter contained identifiable remains, among which 332 euphausiids have been identified at the specific level.

On the basis of detailed knowledge of the vertical distribution of euphausiids in these regions (Roger 1974b), we have selected 99 samples taken with the 3-m Isaacs-Kidd midwater trawl in order to determine the specific composition of the population in the "epipelagic" layer (0-450 m) and the deep layer (450-900 m) by day and by night. We have also made use of recent results on the feeding rhythms of tropical euphausiids (Roger 1975).

The samples originate from three regions of the south tropical Pacific Ocean: Marquesas Islands (10°S, 142°W), New Caledonia (20-22°S, 166-168°E), and Bay of Papua (8°S, 145°E).

Results

Data concerning the position of micronektonic fishes and euphausiids in the food webs which lead to longline tunas are given in Table 1. In general, it appears that euphausiids account for about 12% in volume of the food of the micronektonic fishes which comprise in their turn 60% of

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Table 1. Participation of micronektonic fishes and euphausiids in the trophic webs which lead to longline tunas.

No. of tuna stomach contents analyzed			365
No. of recognizable micronektonic fishes found in the above stomachs*			1,399
Of these 1,399 fishes, No. with identifiable remains in stomach			667=48%
Of these 667 fishes, No. that had eaten euphausiids			179=27%
Mean percentage of the whole diet, in volume, accounted for by euphausiids, in the 179 fishes that had eaten this item			46%
Product of the above two=quantitative importance, in volume, accounted for by euphausiids in the diet of micronektonic fishes which are preyed upon by longline tunas†			12%
Euphausiids found in the 179 stomachs of micronektonic fishes preyed upon by longline tunas	<i>Stylocheiron</i>	Occurrence†	98=55%
		Numbers‡	214=64%
	<i>Euphausia</i>	Occurrence†	20=11%
		Numbers‡	34=10%
	<i>Thysanopoda</i>	Occurrence†	26=15%
		Numbers‡	54=16%
	<i>Nematoscelis</i>	Occurrence†	15=8%
		Numbers‡	30=10%

*The species list of these fishes is given in Legand et al. (1972).

†In addition, most of these fishes eat other crustaceans (mainly copepods and amphipods), except a few species that are ichthyophagous (Legand et al. 1972).

‡No. and percentage of stomachs containing this genus with respect to the number of stomachs containing euphausiids.

§No. of euphausiids belonging to this genus found in the 179 stomachs, with respect to the total number of euphausiids found in these stomachs.

||Not included here: 431 *Euphausia fallax* eaten by three Paralepididae found in the same tuna stomach.

the diet of tunas. In other words, euphausiids are indirectly responsible for 7% of the food of longline tunas, despite the fact that there exists almost no direct predator-prey relationship because of the absence of sufficiently large euphausiids during daytime in the stratum (0-450 m) at which the tunas feed (Roger 1973).

Among the euphausiids ingested by those fishes preyed upon by tunas, *Stylocheiron* species account for 64% of the total num-

ber, *Euphausia* and *Thysanopoda* species together to only 26%. This specific composition is markedly different from that of the whole euphausiid population which inhabits the region and comes to the 0-450-m layer at night (Table 2), but very similar to that of the population remaining in the 0-450-m layer by day (Table 3).

The ratios between the percentages of the nonmigrating *Stylocheiron* which stay at depths above 450 m during the day and the migrating *Euphausia* and *Thysanopoda* which inhabit this layer at night but dwell

Table 2. Euphausiids: percentages (by numbers) of the different genera in the population inhabiting the whole water column, from 43 hauls using a 3-m Isaacs-Kidd midwater trawl by night between 0 and 450 m (almost all the population is concentrated in this layer at night: Roger 1974b).

	10°S, 142°W	20°S, 168°E	22°S, 166°E	Mean
<i>Stylocheiron</i>	37.0	35.5	37.2	36.6
<i>Euphausia</i> and <i>Thysanopoda</i>	55.3	47.6	54.9	52.6
<i>Nematoscelis</i>	6.7	16.4	7.7	10.3
<i>Nematobranchion</i>	1.0	0.4	E	0.5

Table 3. Euphausiids: percentages (by numbers) of the different genera in the population which stays between 0 and 450 m during daytime, from 56 hauls using a 3-m Isaacs-Kidd midwater trawl.

	10°S, 142°W	20°S, 168°E	22°S, 166°E	Mean
<i>Stylocheiron</i>	74.5	68.4	63.8	68.9
<i>Euphausia</i> and <i>Thysanopoda</i>	21.0	27.9	35.1	28.0
<i>Nematoscelis</i>	3.3	3.8	0.9	2.7
<i>Nematobranchion</i>	1.3	0	0.2	0.5

Table 4. Ratios observed between nonmigrating *Stylocheiron* and migrating *Euphausia* and *Thysanopoda*.

Population	S:E+T
Inhabiting whole water column	37:53=0.7
Staying during day between 0 and 450 m	69:28=2.5
Found in stomachs of micronektonic fishes preyed upon by tunas	64:26=2.5

deeper during the daytime are shown in Table 4.

Discussion and conclusions

The foregoing results, together with those previously reported (Roger 1975), lead to the following description of the different links of the food chain.

Longline albacore and yellowfin tunas—Micronektonic fishes ingested by these longline tunas are almost solely epipelagic fishes (Parin 1968; Legand et al. 1972). These tunas very rarely feed on vertically migrating micronektonic fishes which are the main constituents of the deep scattering layers, and which also inhabit the tuna biotope (0–450 m) by night in considerable numbers. Also, as far as albacore and yellowfin tunas are concerned (this is not true for bigeye tuna), longlining is unsuccessful during the night (Legand et al. 1972), so that in the south tropical Pacific these tunas are probably day-feeders.

Epipelagic (0–450 m) micronektonic fishes preyed upon by longline tunas—Euphausiids found in the stomachs of these epipelagic fishes are mainly nonmigrating *Stylocheiron* which stay in this layer during daytime. In contrast, migrating *Euphausia* and *Thysanopoda*, still more abundant than *Stylocheiron* species in these regions but rising to the 0–450-m layer only at night, are more rarely found in the stomachs of these fishes. Therefore, the epipelagic micronektonic fishes preyed upon by longline tunas are also day-feeders; thus they are able to feed only on euphausiids, amphipods, or copepods which stay above 450 m during daytime.

Stylocheiron euphausiids—They are typically day-feeders (Roger 1975), in contrast with *Euphausia* and *Thysanopoda* species which feed either continuously or mainly by night. Unfortunately, we do not know whether the other prey of epipelagic micronektonic fishes (i.e. epipelagic copepods and amphipods) are also day-feeders.

Therefore, it appears that, over the whole length of the food chain considered here, the constituent links exhibit two main similarities: they inhabit the 0–450-m water layer during daytime, and they are day-feeders. This implies the following consequences.

First, each link of the food chain—phytoplankton, small zooplankton → euphausiids → micronektonic fishes → albacore and yellowfin longline tunas has a food source restricted only to the biomass which stays between 0 and 450 m during daytime. In particular, longline tunas (as well as other large pelagic predators which would feed upon the same epipelagic ichthyofauna) have no possibility of benefiting, *through this chain*, from the considerable biomass of migrating species, which are responsible for the deep scattering layers and which are abundantly caught by plankton nets and midwater trawls at night in the epipelagic zone. However, other routes of energy transfer may allow some use of this food source by longline tunas, for example that involving the cephalopods, which comprise nearly 40% of the tunas diet and probably feed to some extent on the migrating fauna. In addition, the boundary between “epipelagic” fauna and the migrating and the deep faunas during the day is, of course, not absolutely strict: the lower part of the former is more or less mixed with the higher parts of the latter, in particular between 400 and 500 m. Mixing also occurs at the time of the diurnal vertical migration (cf. Fig. 1).

Second, the migrating fauna feeds on the epipelagic fauna during the night. As the epipelagic fauna is not feeding at this time, it cannot retrieve the energy given to the migrating fauna. This process is the equivalent of an “energy valve” which promotes

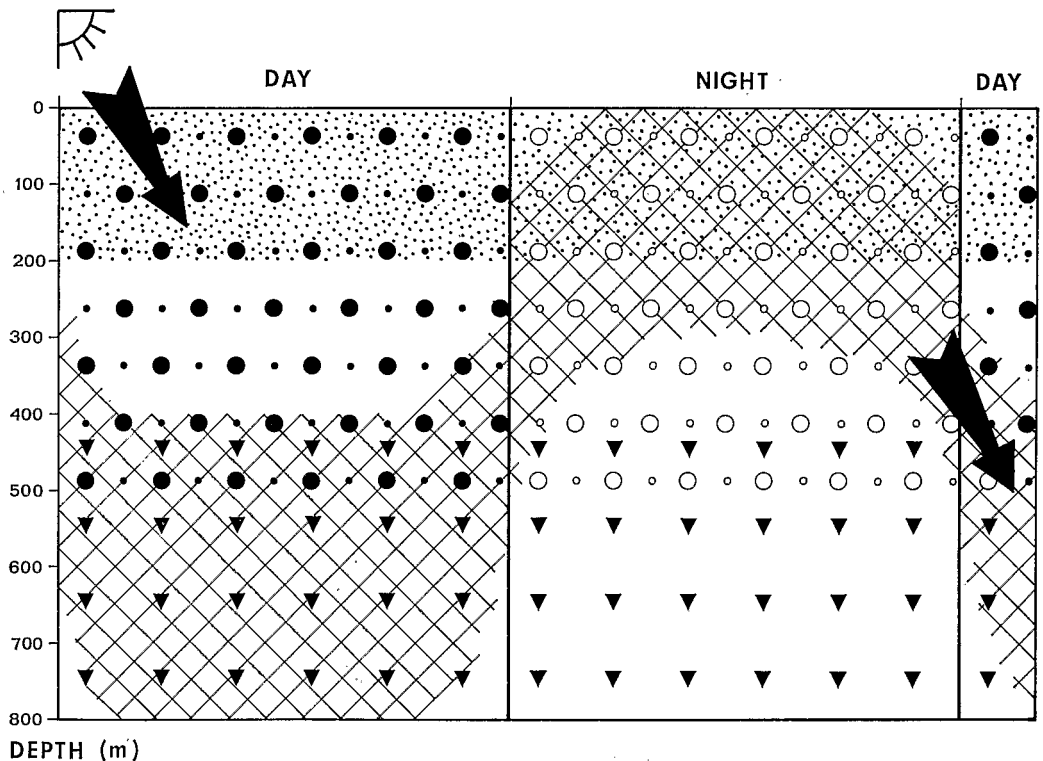


Fig. 1. Diagram tentatively showing the main space-time components of trophic relationships in the pelagic tropical Pacific and resulting preferential way of energy transfer. Stippling—phytoplankton. Arrow—main path of energy transfer. "Epipelagic" (0–450 m) day-feeder fauna (dots—feeding; circles—nonfeeding): small dots and circles—nonmigrant day-feeder zooplankton (e.g. *Stylocheiron* euphausiids); large dots and circles—longline tunas and micronektonic fishes upon which they feed (e.g. *Gempylidae*, *Bramidae*, *Paralepididae*, etc.). Cross-hatching—vertically migrating zooplankton (e.g. *Euphausia* and *Thysanopoda* euphausiids) and micronektonic fishes (e.g. *Myctophidae*, etc.), feeding either continuous or mainly nocturnal. Triangles—nonmigrating deep fauna.

the downward energy transfer and reduces the upward one. If this process does exist in the other food chains of the pelagic tropical Pacific, in particular if the other prey of epipelagic micronektonic fishes (such as epipelagic copepods and amphipods) are also day-feeders, then one can suggest that this mechanism is fundamental as it explains how the deeper layers of the ocean are able to support a fairly large biomass.

The vertical distributions and feeding rhythms of the pelagic food links reported here are tentatively schematized in Fig. 1, together with the main path of energy transfer which they imply.

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