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A seasonal analysis of the nutritional condition of deep-sea macrourid fishes in the north-east Pacific

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Of three common macrourids *Coryphaenoides armatus* and *Coryphaenoides yaquinae* were collected from 1995 to 1998 at an abyssal station, *c.* 220 km west of Point Conception, California in the north-east Pacific (4100 m depth). *Coryphaenoides acrolepis* was collected from 1997 to 1998 in the San Diego Trough (1200 m depth). Energy storage in all three species was primarily in the liver, which was up to 56% lipid (wet mass) and up to 96% triglyceride. No seasonal variation in nutritional condition was found for *C. armatus* or *C. yaquinae*. There was, however, a significant increase in muscle water content and liver lipid content and a significant decline in muscle lactate dehydrogenase activity for *C. armatus* between 1996 and 1998. Potential mechanisms for these interannual shifts are proposed. No seasonal variation in parameters was found for *C. acrolepis* but a small seasonal periodicity in feeding activity may have existed. The seasonal deposition of phytodetritus in the deep sea is of little or no consequence to these fishes.

Key words: macrouridae; seasonality; nutritional condition; diet; energetics; north-east Pacific.

INTRODUCTION

In temperate shallow seas many fishes have a seasonal variation in feeding activity. This cycle can be tied to variation in light, water temperature and reproductive cycles (Bond, 1996). The deep sea is a dark, cold and generally stable environment, which lacks the photic and thermal cues present in shallower waters. A pronounced seasonal cue, however, does exist. With virtually no *in situ* productivity the deep-sea community receives most of its organic matter as sinking particles from the overlying photic zone. In temperate oceans, food input to the deep sea can be in large seasonal pulses of phytodetrital material that occur weeks to months after phytoplankton blooms in the surface waters (Billett *et al.*, 1983; Lampitt, 1985; Tyler, 1988; Smith *et al.*, 1994). These seasonal pulses have been shown to increase microbial and sediment community metabolism (Lochte & Turley, 1988; Pfannkuche, 1993; Smith *et al.*, 1994; Drazen *et al.*, 1998), infaunal organismal abundances (Lambshead & Gooday, 1990; Drazen *et al.*, 1998), and increase the activity of the epibenthic megafauna (Tyler, 1988; Smith *et al.*, 1994). With so many other members of the deep-sea community affected by seasonal pulses of detrital material the question arises: do deep-sea fish exhibit seasonal variation in feeding activity or other energetic parameters?

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Macrourid fishes are among the dominant fishes in the deep-sea. They are often near the top of the food web and can have generalized feeding habits (Pearcy & Ambler, 1974; Mauchline & Gordon, 1984; Gartner *et al.*, 1997; Drazen *et al.*, 2001). Top predators play a vital role in many communities by controlling prey populations, exerting selective pressure, and influencing general community dynamics. Knowledge of seasonal cycles in their feeding activity is important for understanding the energetics of the species as well as defining their relationship with the rest of the community.

Armstrong *et al.* (1991) and Priede *et al.* (1994) have shown that there is a seasonal variation in foraging behaviour (swimming speeds and staying times at artificial bait stations) for the macrourids *Coryphaenoides yaquinae* Iwamoto & Stein and *Coryphaenoides armatus* Hector in the central North Pacific and eastern North Pacific respectively. While these fishes are not eating phytodetritus, their prey populations could vary in abundance, activity or availability in response to phytodetritus input. Various crustaceans, fishes, cephalopods, polychaetes and a few echinoderms are prey, and scavenging is prevalent in *Coryphaenoides acrolepis* Bean (Pearcy & Ambler, 1974; Drazen *et al.*, 2001). Population cycles of these prey species are not well studied but the activity of the epibenthic megafauna, primarily holothuroids, increases in response to seasonal inputs of phytodetritus, which could make them more available as prey (Tyler, 1988; Smith *et al.*, 1994).

Macrourids brought to the surface from great depths have a high frequency of stomach eversion as their large gas bladders expand with decreasing pressure. This unfortunate consequence makes the collection of enough samples for a seasonal analysis of stomach fullness and contents very difficult. Thus, for this study a variety of biochemical indices of the nutritional condition of the fishes were used to estimate feeding activity.

The energy a fish gains from feeding is used in reproduction, metabolism and growth, or is stored as energy reserves (Jobling, 1994). So by estimating these energetic parameters feeding can be determined indirectly. Reproductive state is most often determined using a gonadosomatic index. Biochemical indices have been used to approximate the rest of these parameters. The activities of metabolic enzymes such as citrate synthetase (CS) and lactate dehydrogenase (LDH) correlate well with metabolic rates in fishes (Childress & Somero, 1979; Somero & Childress, 1980). Growth can be approximated by RNA : DNA ratios because growth in fishes is primarily due to protein synthesis (Haines, 1973; Mathers *et al.*, 1992). Proximate composition (lipid, protein, carbohydrate and water) is related to nutritional condition (Love, 1970). Determining the composition of lipids can be important in determining nutritional condition because cell membranes are made of polar lipids but energy is stored as neutral lipids, mostly triglycerides (Love, 1970). Primarily neutral lipids are depleted in the liver of cod *Gadus morhua* L., a shallow water relative of the macrourids, during food shortages and during seasonal reproductive events (Jangaard *et al.*, 1967; Love, 1970; Black & Love, 1986; Smith *et al.*, 1990). Liver lipid content can vary seasonally between 15 and 75% and spawning females and males can lose up to 67% of their liver mass and 25% of their somatic body mass after spring spawning (Jangaard *et al.*, 1967).

In this study, an attempt was made to determine if there are seasonal changes in the feeding activity of *C. armatus*, *C. yaquinae* and *C. acrolepis* from the eastern North Pacific as approximated by biochemical indicators of energetic and nutritional condition. *Coryphaenoides armatus* and *C. yaquinae* are the dominant macrourids on the abyssal plain and *C. acrolepis* is one of the most common and abundant macrourids on the continental slope in the north-east Pacific (Iwamoto & Stein, 1974; Lauth, 1998).

METHODS

Coryphaenoides armatus and *C. yaquinae* were captured from Station M (34°50′N; 123°00′W, 4100 m depth) in the north-east Pacific, *c.* 220 km west of Point Conception, California. This area lies below the California Current, which exhibits large, seasonal variation in surface water chlorophyll *a* concentrations (Michaelsen *et al.*, 1988) and sinking particulate matter (Baldwin *et al.*, 1998). *Coryphaenoides acrolepis* was captured from the San Diego Trough (32°40′N; 117°35′W, 1170 m depth). This area is very close to shore (*c.* 24 km) and surface waters exhibit peaks in primary productivity and zooplankton biomass in summer (Mullin, 1986). No measurements of the sinking particulate matter flux in the San Diego Trough are available, but flux measurements from the neighbouring Santa Catalina Basin exhibit a seasonal cycle (Smith, 1987). Free vehicle baited traps and long lines were used to capture fishes in both locations. *Coryphaenoides armatus* and *C. yaquinae* were captured in February, April and October 1995, January and October of 1996 and in April, August and December 1998. *Coryphaenoides acrolepis* was captured in May, August and December 1997 and in February, June and November 1998.

Onboard the ship, fishes were immediately placed in coolers with ice. *Coryphaenoides armatus* and *C. yaquinae* captured in 1995 were immediately frozen whole at −20° C. These specimens were not used for biochemical analyses. For the rest of the collections samples of white muscle were taken from just below the first dorsal fin and samples of liver tissue were taken from the left lobe of the liver. Tissues were placed in cryovials and frozen in liquid nitrogen (−196° C) for biochemical analyses. These were later transferred to a −70° C freezer in the laboratory. In addition, triplicate samples of both muscle and liver were also placed in preweighed test tubes, sealed with parafilm and frozen at −20° C, for later water content determination. Fish lengths (total length, L_T, and pre-anal fin length (L_{PA}) were taken and each fish was wrapped in plastic and frozen at −20° C. In the laboratory, fish (M), liver (M_L) and gonad (M_G) masses were measured.

Reproductive state was estimated using a simple gonadosomatic index (I_G) from $I_G = 100\ M_G\ M^{-1}$. For *C. acrolepis* the dominant oocyte diameter in a *c.* 0·5 g subsample of one of each of the ovaries of the fish was determined. Each mature female was determined as either spent, ripening or developing, according to the criteria of Stein & Pearcy (1982). Ripening ovaries were those with many large oocytes (1–1·4 mm) and spent ovaries were often flaccid and had many small oocytes (0·1–0·2 mm) with a few large, loose oocytes.

White muscle enzyme activities and RNA and DNA concentrations were determined on triplicate homogenates. LDH and CS were assayed using the methods of Yancey & Somero (1978) and Srere (1969), respectively. Assays were run at 3° C for *C. armatus* and *C. yaquinae* and at 10° C for *C. acrolepis*, temperatures close to the *in situ* temperature experienced by each species. RNA and DNA concentrations were determined using the fluorometric technique of Bentle *et al.* (1981) as modified by Lowery & Somero (1990). DNA purified from calf thymus (Sigma D-3664) and RNA Type III from yeast (Sigma R-7125) were used as standards.

A proximate analysis of the tissues was performed. Water content was determined by the difference between wet mass and dry mass after lyophilizing the samples. Protein, carbohydrate and lipid assays were performed in triplicate on tissue homogenized in

distilled water. The bicinchoninic acid (BCA) protein assay (Smith *et al*., 1985) and the Dubois *et al*. (1956) carbohydrate assay were used with bovine serum albumin and *d*-glucose as standards, respectively. Lipids were extracted according to Bligh & Dyer (1959) and lipid composition was determined using the Iatroscan technique which combines thin layer chromatography to separate lipid classes and flame ionization for detection and quantification (Fraser *et al*., 1985; Volkman & Nichols, 1991). Cholesteryl oleate, triolein, oleic acid, cholesterol, diolein and phosphatidylcholine were used as standards for steryl esters (SE) , triglycerides (TAG), free fatty acids (FFA), sterols (ST), diglycerides (DAG) and phospholipids (PL), respectively. Standards were run for each set of 10 SIII chromorods and the best fitting standard curves were either linear or power functions. Lipids were concentrated, resuspended in chloroform and spotted (1 µl) in duplicate. Rods were developed in 85 : 15 : 0·01 (muscle lipids) or 90 : 10 : 0·01 (liver lipids) of hexanes : diethyl ether : formic acid for 20–25 min. Rods were dried for 8–10 min in an oven at 110° C prior to scanning on a Mark V Iatroscan. Each frame was scanned once to quantify the lipid classes and a second time to clean the rods in preparation for the next sample.

The effect of fish length on condition factors was assessed. At a given length the mass of a fish can be used as a condition factor (Smith *et al*., 1990). Therefore, fish length is a better estimate of fish size independent of condition. Regressions between condition factors and L_{PA} were made. Where significant scaling relationships were found condition factors were standardized to the mean L_{PA} of the fish using power functions. The relationships between L_{PA} and M_L were not linear but a power function so a standard liver mass (g) was calculated from the mean size of the fish. After any size standardization, seasonal variation in parameters was assessed using Kruskal–Wallis ANOVA and Mann–Whitney *U*-tests for independent comparisons. Correlation between condition factors was made using Spearman-rank correlation.

RESULTS

The abyssal species *C. armatus* and *C. yaquinae* showed no seasonal trends in I_G [Fig. 1(a),(b)]. One large female *C. armatus* had well developed gonads in February of 1995, but the rest of the females never exceeded a I_G of 1·2%. Most of the female *C. yaquinae* were small and I_G was low throughout the collection period.

Nutritional condition indices for *C. armatus* did not show any seasonal changes but some parameters did change over the whole sampling period (Fig. 2). RNA : DNA ratios were fairly consistent with the exceptions of high and variable values for December 1998. RNA did not show any relationship with fish size but enzyme activities were related to L_{PA}: CS=5·65 $L_{PA}^{-0·746}$, r^2=0·15, n=69 and LDH=37·52 $L_{PA}^{0·337}$, r^2=0·07, n=69. Size standardized CS activity remained constant but LDH activity changed significantly with lower activities in 1998 [Kruskal–Wallis ANOVA, P<0·05; Fig. 2(a)]. Water content was at a low in 1996 [Kruskal–Wallis, ANOVA, P<0·05; Fig. 2(b)]. Muscle lipids showed changes similar to those of LDH with lower lipid in 1998 [Kruskal–Wallis, ANOVA, P<0·05; Fig. 2(e)]. Not only were lipid concentrations lower but lipid composition changed as well. Phospholipid content was significantly higher [Kruskal–Wallis, ANOVA, P<0·05) and most of the neutral lipid classes were lower in 1998 [Fig. 3(a)].

The liver of *C. armatus* was predominantly water and lipid [Fig. 2(g)–(j)] with TAGs making up *c*. 95% of the lipids [Fig. 3(b)]. Liver mass and composition were significantly related to L_{PA} with the largest fish having the largest most lipid rich livers. The largest *C. armatus* had livers 14–18% of body mass which were

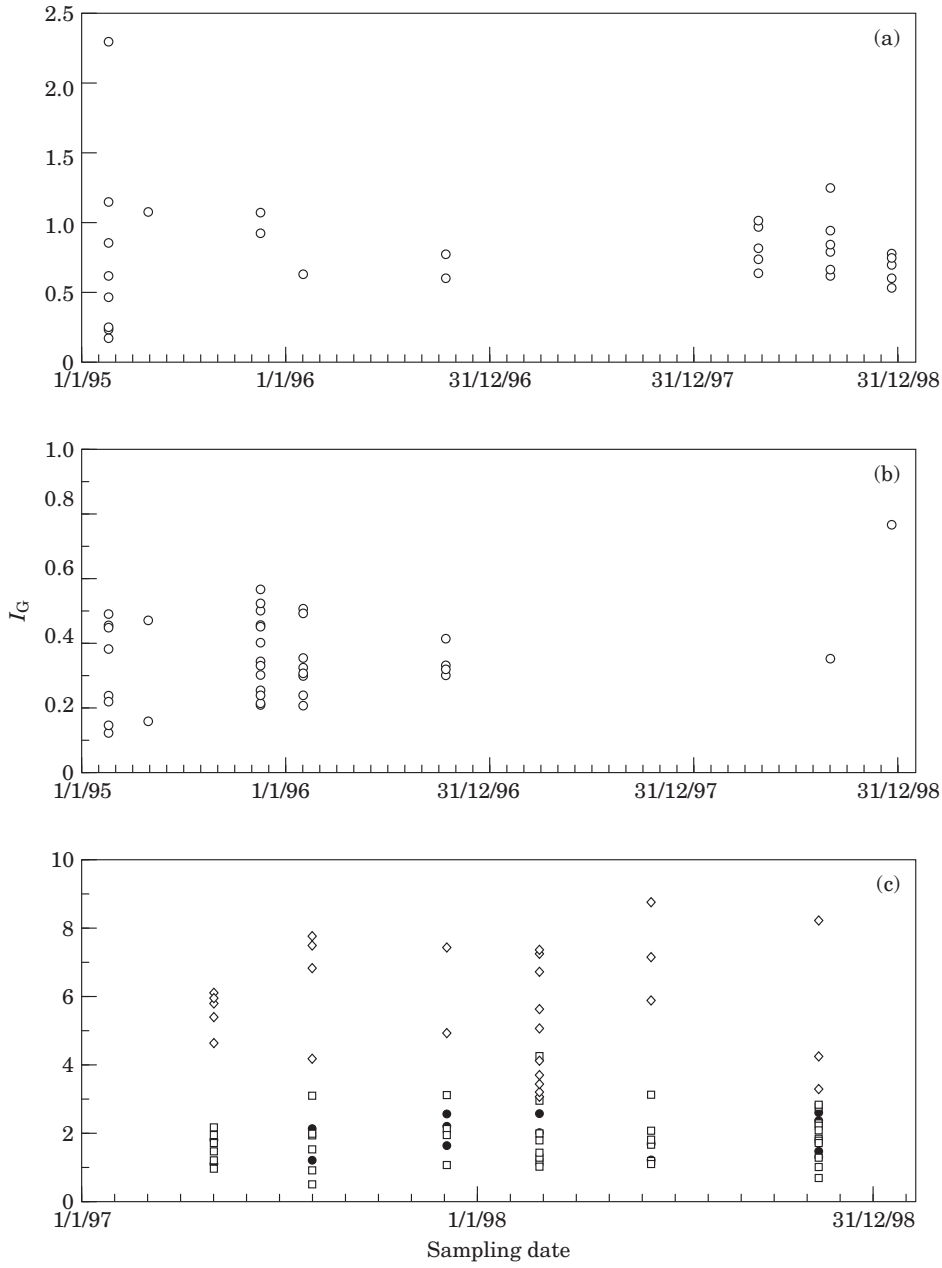

FIG. 1. Gonadosomatic index for (a) *Coryphaenoides armatus*, (b) *C. yaquinae* and (c) *C. acrolepis* females. ●, spent; □, developing; ◇, ripening.

comprised of 56% lipid. Once these relationships were taken into account, the standardized liver mass did not significantly vary between sampling dates and variability was very high [Fig. 4(a)]. Liver lipid concentration was significantly different between sampling periods with higher values in 1998 [Kruskal–Wallis, ANOVA, $P<0{\cdot}05$, Fig. 2(j)]. Water content [Fig. 2(g)] declined as lipid increased

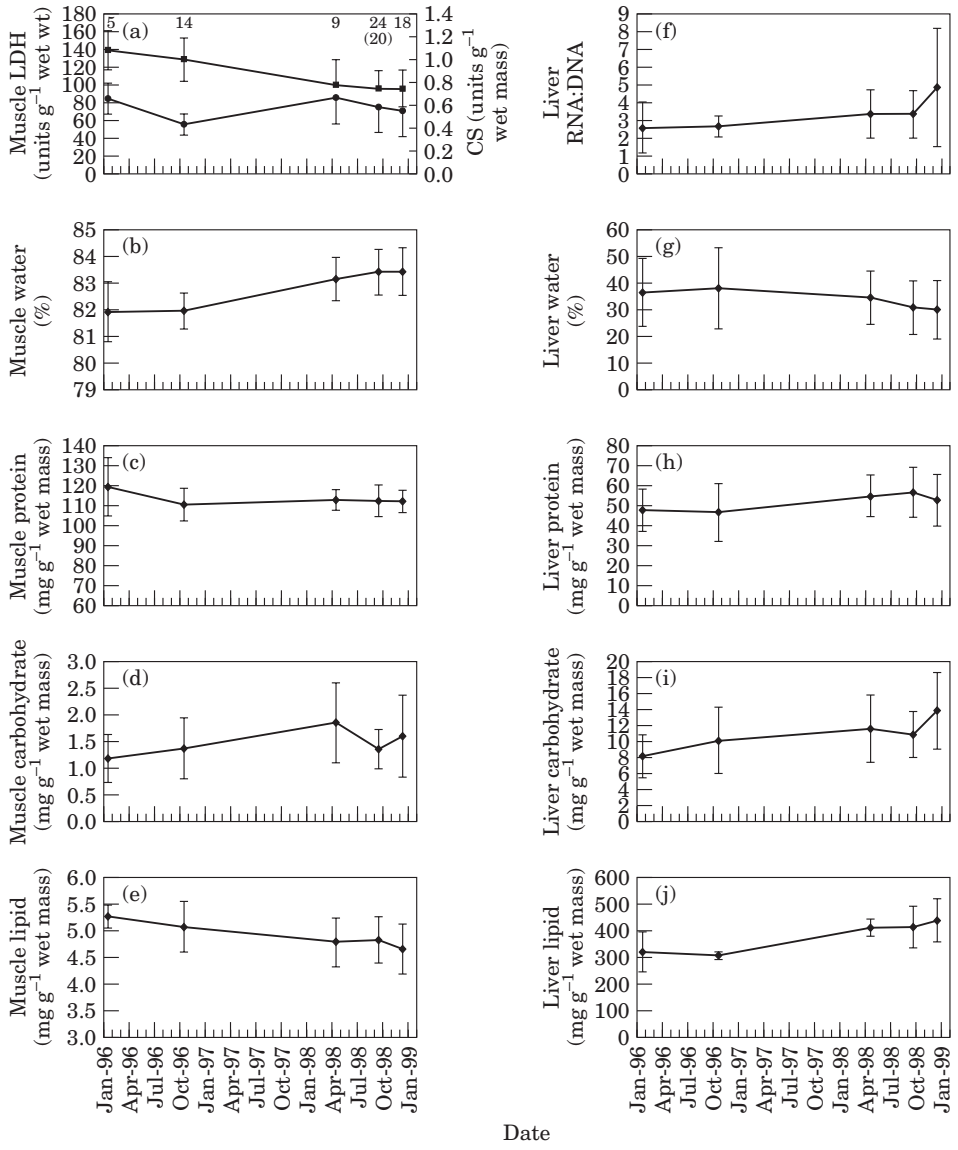

FIG. 2. Indices of nutritional condition for *Coryphaenoides armatus*. (a) Muscle LDH (■) and CS (●); (b) muscle water; (c) muscle protein; (d) muscle carbohydrate; (e) muscle lipid; (f) muscle RNA : DNA; (g) liver water; (h) liver protein; (i) liver carbohydrate; (j) liver lipid. Means ± S.D. The numbers above the points in (a) are the number of samples for each collection period. Where sample sizes differ for muscle and liver indices, sample size for liver indices is given in parentheses.

but this change was not significant. Liver lipid composition was dominated consistently by TAG [Fig. 3(b)]. In September 1998 TAG was a little lower and variability was considerably higher than for other sampling periods [Fig. 3(b)]. This variability was due to a single individual with a very small liver and little TAG (2·7%).

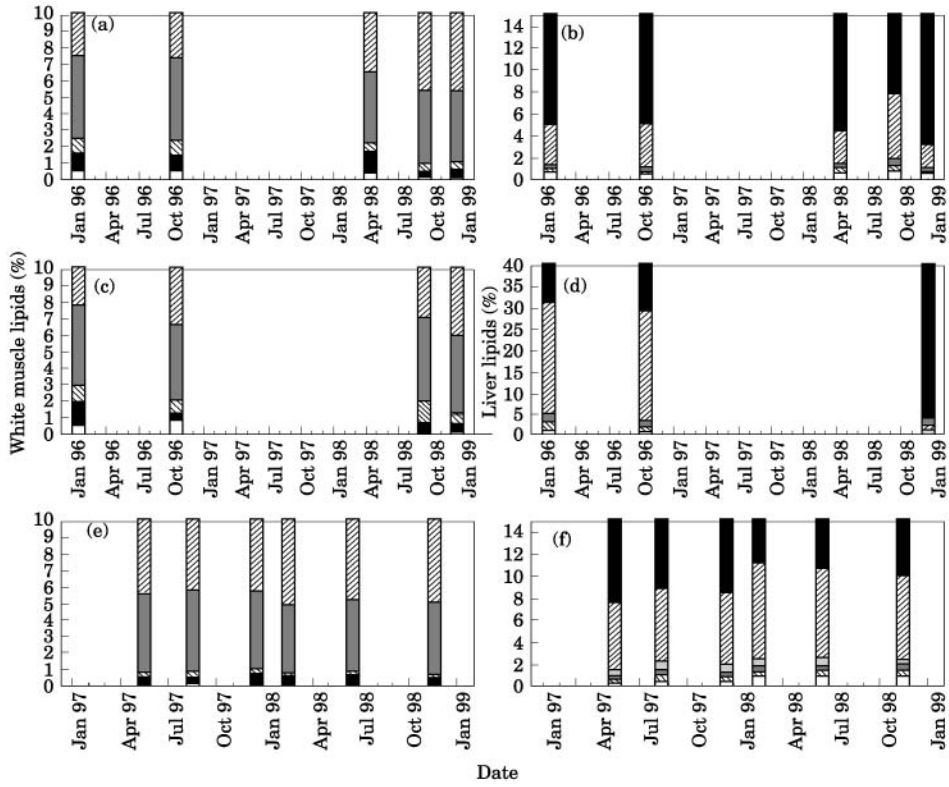

FIG. 3. Muscle and liver lipid per cent composition for *Coryphaenoides armatus*, (a) (b), *C. yaquinae* (c) (d) and *C. acrolepis* (e) (f). ■, TAG; ▨, PL; □, DAG; □, ST; ▧, FFA; □, SE.

A seasonal analysis of nutritional condition for *C. yaquinae* was difficult to make as only three specimens were captured in 1998 and no specimens in the spring of that year. Enzyme activities were related to L_{PA}, as for *C. armatus*, CS=202·77 $L_{PA}^{-2·095}$, r^2=0·44, n=17; LDH=0·74 $L_{PA}^{1·722}$, r^2=0·38, n=17). Liver mass but not composition was correlated to L_{PA}. After indices were scaled for L_{PA}, comparisons between January and October of 1996 were made but no significant differences in condition indices were found (Mann–Whitney U-tests, P>0·05; Table I). Using standardized liver mass, comparisons were made over 2 years but no significant variation was found [Fig. 4(b)]. Standardized liver mass and liver lipid content and composition [Fig. 3(d)] were highly variable with some fish having large livers with high TAG content and others having small livers with little TAG.

As for the abyssal macrourids, there were few significant changes in indices of nutritional condition for *C. acrolepis* captured in the San Diego Trough (Fig. 5). While liver size increased with fish size composition did not change significantly. Therefore, liver mass was standardized to a mean L_{PA}, but not liver composition. Standardized liver mass was slightly higher for fish captured during May and August of 1997 [Fig. 4(c)] but liver composition [Fig. 5(g)–(j)] and liver lipid composition [Fig. 3(f)] did not change. Liver lipid content was as much as 45% with liver mass *c*. 5% of the body mass. Small amounts of DAGs were present in

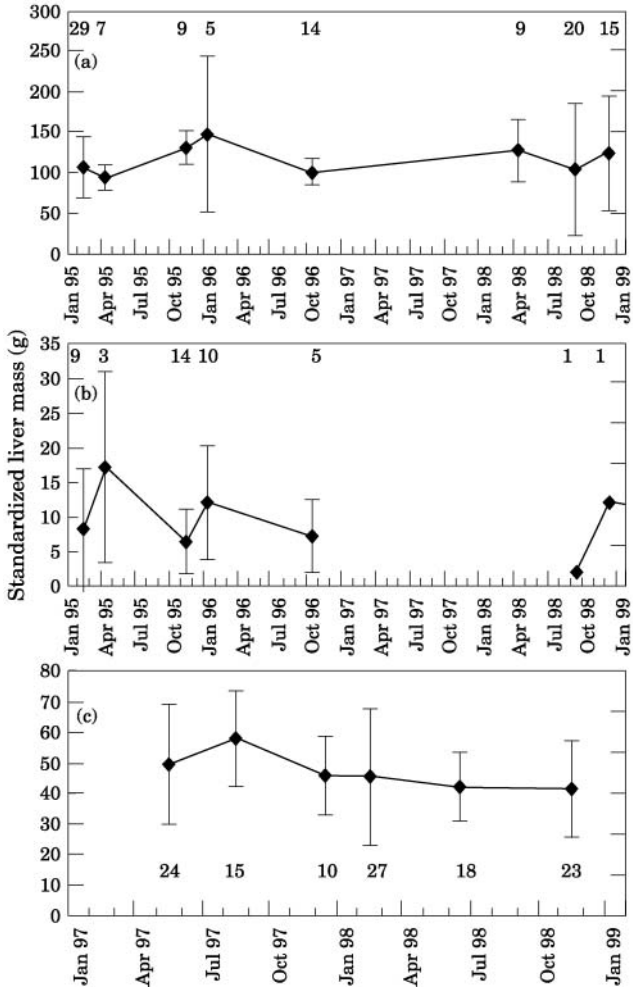

FIG. 4. Standardized liver mass for (a) *Coryphaenoides armatus*, (b) *C. yaquinae* and (c) *C. acrolepis*. Numbers represent sample size.

the livers of *C. acrolepis* [Fig. 3(f)] but not in the livers of the other two species. RNA : DNA ratios and enzyme activities [Fig. 5(a),(f)] were also rather constant. Muscle water content was lower during May and August of 1997 [Fig. 5(b)] but other muscle composition did not change [Fig. 5(c)–(e)]. Muscle lipid composition was very constant [Fig. 3(e)].

I_G for *C. acrolepis* was much higher than for either abyssal macrourid and no seasonal cycle could be seen [Fig. 1(c)]. Females with spent ovaries had very low I_G (1–2%) compared to ripening females but low I_G was also found for females that had developing ovaries. Females with ripening ovaries ($n=22$) were present in all collections but no ripe individuals were captured. Females with spent ovaries ($n=14$) were also found in every collection. Spent females had a standardized liver mass of $42{\cdot}4 \pm 10{\cdot}9$ g which is significantly lower than that of the females with ripening ovaries, $57{\cdot}3 \pm 16{\cdot}7$ g ($P<0{\cdot}05$).

TABLE I. Indices of nutritional condition for *Coryphaenoides yaquinae*. Means, S.D. and sample sizes are given

Sampling date	31/1/1996			11/10/1996			1/9/1998		20/12/1998		
Nutrional index	Mean	S.D.	*n*	Mean	S.D.	*n*	Mean	*n*	Mean	S.D.	*n*
Muscle											
RNA : DNA	2·03	0·36	10	2·42	0·71	5	1·50	1	4·56	0·57	2
CS (units g^{-1} wet mass)	0·68	0·20	10	0·73	0·21	5	0·82	1	0·61		1
LDH (units g^{-1} wet mass)	78·36	15·50	10	85·67	24·18	5	67·72	1	47·37		1
Muscle composition											
Water content (%)	83·26	0·91	9	82·01	0·40	5	83·04	1	84·26	0·14	2
Protein (mg g^{-1} wet mass)	107·36	14·93	9	103·23	10·35	4	115·20	1	108·09	9·33	2
Carbohydrate (mg g^{-1} wet mass)	1·12	0·33	9	1·21	0·21	5	1·10	1	1·11	0·04	2
Lipid (mg g^{-1} wet mass)	5·07	0·38	9	4·80	0·37	5	5·01	1	4·59	0·35	2
Liver composition											
Water content	56·21	21·10	9	42·63	19·90	5			45·00		1
Protein (mg g^{-1} wet mass)	70·94	20·13	9	76·68	21·44	5			57·49		1
Carbohydrate (mg g^{-1} wet mass)	14·30	13·41	9	8·59	4·35	5			11·71		1
Lipid (mg g^{-1} wet mass)	116·39	103·30	9	102·07	97·06	5			344·34		1

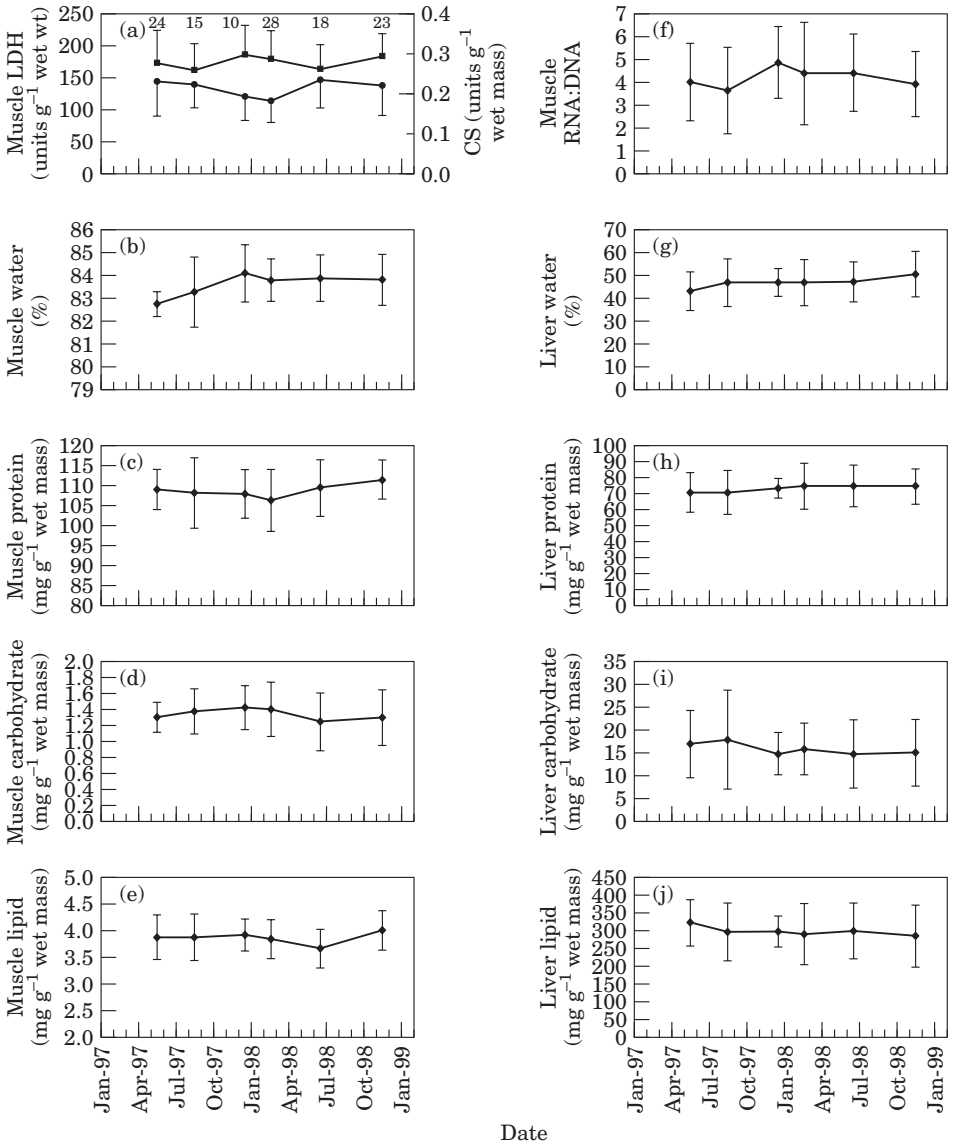

FIG. 5. Indices of nutritional condition for *Coryphaenoides acrolepis*. (a) Muscle LDH (■) and CS (●); (b) muscle water; (c) muscle protein; (d) muscle carbohydrate; (e) muscle lipid; (f) muscle RNA : DNA; (g) liver water; (h) liver protein; (i) liver carbohydrate; (j) liver lipid. Means ± S.D. The numbers above the points in (a) are the number of samples for each collection period.

DISCUSSION

Coryphaenoides armatus and *C. yaquinae*, the abyssal species examined in this study, lacked any seasonal periodicity in nutritional or reproductive status. Little is known of reproduction of *C. yaquinae* but it has been suggested that *C. armatus* is semelparous as few ripe females and no spent individuals have been collected (Stein & Pearcy, 1982). No ripe females were found in this study either

and the highest I_G was 2·3%. If these fishes are semelparous then no seasonal variation in nutritional condition will be seen due to reproductive events. Instead, seasonal variation in nutritional condition would result from changes in feeding activity, metabolism and growth.

Seasonal variation in foraging behaviour has been described for both *C. armatus* (Priede *et al.*, 1994) and *C. yaquinae* (Armstrong *et al.*, 1991) and a pronounced seasonal input of organic matter to the deep-sea community is well documented at Station M (Smith *et al.*, 1994; Smith & Druffel, 1998). These investigators found that fishes had higher swimming speeds and shorter staying times at bait stations in autumn after the annual deposition of phytodetritus to the seabed. Staying time at the bait station was related to food supply. Using optimal foraging theory it is argued that animals experiencing a lower food supply stay longer where they find it (Priede & Bagley, 2000). Macrourid fishes probably do not eat phytodetritus but it has been shown to stimulate the activity of the epibenthic megafauna (Smith *et al.*, 1994), some of which are prey of these fishes (Pearcy & Ambler, 1974; unpubl. data). The seasonal variation in swimming speeds found by Priede *et al.* (1994) was not evident in the enzyme activities, biochemical correlates to metabolic activity, measured in this study. In addition, lower energy reserves during the spring, which would suggest lower food supplies and use of stored energy, were not found. Instead significant variations in enzyme activities, muscle water content and liver lipids were found between years. The problem with the studies of foraging behaviour is that the measurements are taken for different seasons in different years (Priede & Bagley, 2000). Therefore, if the differences in foraging behaviour are actually due to interannual variability this could be easily misinterpreted as a seasonal cycle.

The data for the abyssal species in this paper are difficult to interpret but two plausible explanations are proposed. First, the fishes could be preparing to spawn. Muscle composition of *C. armatus* had lower water content and higher LDH activity in 1996 compared to 1998. This would indicate a higher nutritional condition and greater metabolic activity in 1996. In 1998, however, liver lipids were higher than in 1996. In many fishes including cod, an increase in energy storage in the liver occurs before and during the first stages of gonadal development (Love, 1970). However, I_G does not increase in 1998. Second, interannual variation in food supply could affect the fishes energetic status. The year 1997 was an El Niño year. Perhaps, a resulting reduction in sinking phytodetritus (there was a hiatus in sampling particle flux during 1997) impacted the deep-sea community and the prey populations of *C. armatus*. This explains the reductions in enzyme activities and increases in muscle water content but not the increased liver lipids. Long-time series investigations will be required to determine whether the dominant forces affecting the feeding and energetics of these macrourid fishes are interannual instead of seasonal.

No seasonality in nutritional condition or reproductive status of *C. acrolepis* was found. Matsui *et al.* (1990) reported a preponderance of spent female *C. acrolepis* off southern California in the spring and summer but individuals with ripening ovaries were found all year round and specimens with ripe ovaries were never found. Stein & Pearcy (1982) found only three ripe female *C. acrolepis*, one in April and two in September. They suggest that this species may spawn semi-annually. Recently, collection of more data has suggested that

this species is a continuous spawner with a possible peak in the autumn (D. L. Stein & R. C. Albright, unpubl. data). In accordance with the latter study, this analysis revealed no significant variation in mean I_G of *C. acrolepis,* and specimens with ripening eggs and specimens with spent ovaries were found throughout the year. In the deep-sea where food is scarce relative to shallow water, *C. acrolepis* might have to invest energy into gonads over periods of time >1 year so they may only be ready to reproduce every few years. Consequently, only those members of the population that spawned would show a seasonal decline in such factors as I_G and liver energy stores and this result would probably not be seen as a seasonal signal. In fact the I_G and standardized liver mass of spent females is significantly lower than that of ripening individuals (Mann–Whitney *U*-test; $P<0{\cdot}05$). If all the females were spawning synchronously a seasonal decline in gonad and liver size would be seen.

Using otolith margin analyses, seasonal growth cycles have been found in several macrourid fishes that had their fastest growth in the summer (Morales-Nin, 1990; Massuti *et al*., 1995) or the winter (Gordon & Swan, 1996). Recently radiometric validation of the periodicity of otolith ring formation has been made for several deep-sea fishes including *C. acrolepis* (Andrews *et al*., 1999). The index of growth, RNA : DNA ratios, however, did not significantly vary for this species. Based on Andrews *et al*.'s (1999) growth curve the average age for the *C. acrolepis* collected in this study was 45 years (average size=23 cm L_{PA}). At this age growth slows considerably and perhaps the amplitude of any seasonal variability is reduced. RNA : DNA ratios are affected by the recent feeding history of a fish (Black & Love, 1986; Lowery & Somero, 1990). If recent feeding activity was variable then this could add enough variability to mask small, seasonal changes in growth rates. The RNA : DNA ratios in this study have an average CV of 43%. Fishes kept under common nutritional conditions in the laboratory have much lower variability in RNA concentrations, 14% (Yang & Somero, 1996), and RNA : DNA ratios, *c*. 20% (Lowery & Somero, 1990). Seasonal variation in feeding activity in *C. acrolepis* cannot be ruled out. Previous work has documented seasonal growth in this species, which in the absence of seasonal reproduction, energy storage and metabolism implies that feeding must vary to account for the cycle in expenditure.

The present results are very similar for both the abyssal and bathyal macrourids. *Coryphaenoides acrolepis* was collected in the San Diego Trough, shallower waters much closer to shore than Station M. *Coryphaenoides acrolepis* is therefore closer to the strong seasonal environments of the continental shelf and epipelagic zone. As for the abyssal species, however, indices of nutritional condition do not indicate strong seasonality in energetic processes. Only otolith work (Andrews *et al*., 1999) implies a seasonal pattern in growth.

The apparent lack of strong seasonality in energetic processes can be explained in several ways. The variability in nutritional condition could be of such low amplitude that with the present sampling frequency it is undetectable. As discussed above, this may be the case with growth for *C. acrolepis*. Seasonal periodicity in nutritional condition is very pronounced in cod (Jangaard *et al*., 1967; Love, 1970; Black & Love, 1986; Smith *et al*., 1990). Despite the similarity in lipid storage between cod and the macrourids in this study, no seasonal depletions of liver lipids or mass were evident. Even much less dramatic hepatic

changes would have been detected in this study but greater sampling frequency and sample sizes would be required to detect the smallest changes in condition.

A lack of strong seasonality in energetic processes could also reflect the high trophic position of the macrourids studied. The impacts of the seasonal deposition of phytodetritus on the deep-sea benthos may be damped by many levels in the food web. At intermediate levels in the deep-sea food web the lack of seasonal cycles in energetic processes is common. Seasonality in reproduction and growth of some deep-sea megafaunal invertebrates has been shown but it is absent in many (Tyler, 1988). In the San Diego Trough, only two of 12 invertebrate species examined exhibited seasonal reproduction (Rokop, 1974). Neither *C. acrolepis* nor *C. armatus* feed exclusively on benthic megafaunal invertebrates; they also consume midwater fishes and squid. For *C. acrolepis* these prey include vertically migrating organisms such as myctophids (Drazen *et al.*, 2001) which may exhibit seasonal population cycles. Finally, it is possible that the generalized feeding habits of these fishes allow them to switch to whatever food is available. Therefore, even if some prey exhibit seasonal cycles in abundance or availability, this does not affect the nutritional and energetic state of the macrourids in this study.

In conclusion, the energetic cycles of these deep-sea macrourids appear to be different from those of shallow water fishes. Seasonal variation in feeding and energetics appear either small or non-existent in these deep-sea fishes. *Coryphaenoides armatus* experienced an interannual shift in nutritional condition whereas *C. acrolepis* may have a low-amplitude seasonal shift in growth. Despite the importance of seasonal inputs of phytodetritus to the deep-sea on a variety of sediment infauna and epifauna, it appears that these effects have little impact on the top predators, the macrourids.

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