

Chapter 2

Protein Requirement—‘*Only Meat Makes You Strong*’



Abstract Proteins represent the dominant biomass of aquatic animals; consequently, proteins are significant nutrients and energy sources with digestive efficiencies between 60 and almost 100%. For most aquatic animals, the quantity of prey available is typically the nutritional bottleneck. A deficiency of dietary protein or amino acids has long been known to impair immune function and increase the susceptibility of animals to infectious disease. In addition to function as energy source, free amino acids can act as osmolytes. The average dietary protein requirement of fishes is 42%; that of invertebrates appears to be below this value. Protein requirement depends on environmental factors, such as salinity and temperature, as well as trophic level and content of the other macronutrients. Interactions with other macronutrients, however, are not yet adequately considered. Adverse effects occur in animals fed deficient or excess proteinaceous diets. Biomolecular modes of action of hyperproteic diets are beginning to be understood; impairment of the immune system is central. Finally, this chapter points out gaps of protein nutrition in aquatic animals.

From a quantitative perspective, amino acids (AAs), either free or combined in macromolecules (peptides, proteins), represent the dominant dry mass component of most living systems. In general, aquatic animals consume nearly every type of food ranging from sediment, detritus, fruits, algae, or wood to slime, scales, blood, mollusks, echinoderms, arthropods, mammals, and other fishes in order to meet their needs.

Fishes efficiently digest protein from most feedstuffs with high efficiency of some 60% to almost 100% (Table 2.1). Considering that 65–75% of their carcass dry mass is protein, fishes need to absorb protein efficiently from food, if for nothing else, tissue maintenance and growth (although many carnivorous fishes metabolize AAs for energy). Noteworthy, the dietary protein requirement of aquatic invertebrates lies in the same range (Table 2.2).

Table 2.1 Summarized digestive efficiency of protein in selected fishes of different trophic levels consuming artificial feeds. (From German (2011), with permission from Elsevier)

Species name, common name	Trophic level (feeding habit)	Efficiency, %
<i>Cyprinus carpio</i> , Common carp	Omnivorous/benthivorous	80–93
<i>Dicentrarchus labrax</i> , European seabass	Carnivorous	62–97
<i>Ictalurus punctatus</i> , Channel catfish	Carnivorous/omnivorous	66–87
<i>Oncorhynchus mykiss</i> , Rainbow trout	Carnivorous	68–96
<i>Oreochromis niloticus</i> , Nile tilapia	Omnivorous/detritivorous	88–96
<i>Pagrus major</i> , Red seabream	Carnivorous	88–96

Animal prey is richer in proteins and more digestible than plant or detrital materials (Fig. 2.1). However, the quantity of prey available is typically the bottleneck. It is common for fishes to ingest well below 5% of body mass per day when feeding on invertebrate prey. This is consistent with the notion that morphology and behavior of fishes feeding extensively on invertebrates are adapted to optimize energy gain (Bowen et al. 1995). Algae, aquatic macrophytes, and detritus are all inferior to fishes and aquatic invertebrates as sources of protein and energy. Furthermore, protein supply is the major constraint for detritivores.

Dietary protein is the major and most expensive component of formulated aquafeeds; fishmeal is generally considered to be the most ideal protein source for aquatic animals (Li et al. 2009). A deficiency of dietary protein or AAs has long been known to impair immune function and increase the susceptibility of animals to infectious disease (Li et al. 2007). Aquatic invertebrates, fish eggs, embryos, and larvae are no exception, and several studies point out the importance of AAs for their catabolic and anabolic energy metabolism. To demonstrate this importance, we refer to hybrid striped bass and zebrafish: glutamate (Glu) and glutamine (Gln) are more actively oxidized in the proximal intestine, liver, and kidney of fish than glucose and palmitate. Glu provides more energy than Gln in all tissues except in the liver where Gln serves as the main metabolic fuel. In the skeletal muscles, Glu is the preferred nutrient to generate adenosine triphosphate (ATP). Together, Glu plus Gln (plus leucine, Leu) contributes to about 80% of ATP production in the fish tissues (Jia et al. 2017).

In addition to the function of AAs as energy source, free AAs (fAAs), individually or in concert, can act as osmolytes in habitats of varying salinity as recently shown in Amazon river prawn *Macrobrachium amazonicum* (Mazzarelli et al. 2015) and San Francisco brine shrimp *Artemia franciscana* (Zadehmohseni et al. 2020).

Table 2.2 Typical crude protein requirement in selected aquatic animals

Species	Requirement, % dry matter	References
Scientific name, common name		
<i>Invertebrates</i>		
<i>Astacus leptodactylus</i> , Narrow clawed crayfish	30	Ghiasvand et al. (2012)
<i>Babylonia areolate</i> , Ivory shell	45	Zhou et al. (2007)
<i>Cherax quadricarinatus</i> , Red claw crayfish	25	Pavasovic et al. (2007)
<i>Eriocheir sinensis</i> , Chinese mitten crab	35–50	Pan et al. (2005)
<i>Farfantepenaeus aztecus</i> , Northern brown shrimp	40–51	In Shiau (1998)
<i>F. californiensis</i> , Yellow leg shrimp	35	
<i>Fenneropenaeus indicus</i> , Indian prawn	43	
<i>F. merguensis</i> , Banana shrimp	34–42	Sedgwick (1979)
<i>F. chinensis</i> , Chinese white shrimp	45	Wu and Dong (2002)
<i>Haliotis asinina</i> , Ass’s-ear abalone	27	Bautista-Teruel et al. (2003)
<i>H. discus hannai</i> , Disk abalone	30	Ma et al. (2020)
<i>H. fulgens</i> , Green abalone	40.4–44.1	Gómez-Montes et al. (2003)
<i>H. iris</i> , Black-footed abalone	38.8–42.3	Tung and Alfaro (2011)
<i>H. laevigata</i> , Greenlip abalone	24–~35 ^a	Stone et al. (2013)
<i>H. midae</i> , South African abalone	22–26	Green et al. (2011)
<i>Jasus edwardsii</i> , Southern rock lobster	29–31	Ward et al. (2003)
<i>Limulus polyphemus</i> , Atlantic horse-shoe crabs	8.7 ^b	Tzafirir-Prag et al. (2010)
<i>Litopenaeus setiferus</i> , Northern white shrimp	28–44	Andrews et al. (1972), Guzman et al. (2001)
<i>L. stylirostris</i> , Western blue shrimp	27–40	Rosas et al. (2001), Martinez-Cordova et al. (2003)
<i>L. vannamei</i> , Pacific white shrimp	25–48 79–86	Smith et al. (1985)
<i>Lytechinus variegatus</i> , Green sea urchin	~20	Hammer et al. (2006)
<i>Macrobrachium americanum</i> , Cauque river prawn	37	Méndez-Martínez et al. (2017)
<i>M.idea</i> , River prawn	27–40	Sethuramalingam and Gideon (2003)
<i>M. malcolmsonii</i> , Monsoon river prawn	35	Thirumurugan and Subramanian (2004)
<i>M. nipponense</i> , Oriental river prawn	33	Zhang et al. (2017a)
@ 20°C	38	Lv et al. (2021)
@ 25°C	42	
@ 30°C	34	
<i>M. rosenbergii</i> , Giant river prawn	13–40	Gomez et al. (1988), Felix and Prince Jeyaseelan (2006)

(continued)

Table 2.2 (continued)

Species	Requirement, % dry matter	References
<i>Marsupenaeus japonicus</i> , Kuruma shrimp	34–57	Deshimaru and Yone (1978), Koshio et al. (1993)
<i>Penaeus monodon</i> , Black tiger shrimp	33–50	Alava and Lim (1983), Syama Dayal et al. (2003)
<i>Pomacea urceus</i> , Edible apple snail	20	Ramnarine (2004)
<i>Portunus trituberculatus</i> , Swimming crab	52	Jin et al. (2013)
<i>Procambarus clarkii</i> , Red swamp crayfish	30	Hubbard et al. (1986)
<i>Scylla serrata</i> , Giant mud crab	32–45	Catacutan (2002), Unnikrishnan and Paulraj (2010)
<i>Sipunculus nudus</i> , Peanut worm	43	Zhang et al. (2015)
<i>Fishes</i>		
<i>Acanthopagrus macrocephalus</i> , Blackhead bream	41	Zhang et al. (2010)
<i>Acipenser baerii</i> ♀ × <i>A. gueldenstaedtii</i> ♂, Hybrid sturgeon	34–37	Guo et al. (2012)
<i>Anabarrilius grahami</i> , Fuxian minnow	37	Deng et al. (2013)
<i>Anabas testudineus</i> , Climbing perch	40	Hossain et al. (2012)
<i>Anguilla anguilla</i> , European eel	36–45	De La Higuera et al. (1989)
<i>A. japonica</i> , Japanese eel	44	Okorie et al. (2007)
<i>A. rostrata</i> , American eel	47	Tibbetts et al. (2000)
<i>Arapaima gigas</i> , Pirarucu	~49	Rodrigues et al. (2019)
<i>Barbonymus altus</i> , Red tailed tinfoil	40	Elangovan and Shim (1997)
<i>B. gonionotus</i> , Silver barb	32	Mohanta et al. (2008)
<i>Bidyanus bidyanus</i> , Silver perch	37	Yang et al. (2002)
<i>Brachymystax lenok</i> , Manchurian trout	~44	Lee et al. (2001)
<i>Brycon orbignyanus</i> , Piracanjuba	~31	De Borba et al. (2003)
<i>Candidia barbata</i> , Lake Candidus dace	32	Shyong et al. (1998)
<i>Carassius auratus</i> , Goldfish	29	Lochmann and Phillips (1994)
<i>C. gibelio</i> , Gibel carp	juveniles	Ye et al. (2017b)
	pre-adults	
<i>Gibelion (Catla) catla</i> , Major Indian carp, catla	30	Renukaradhya and Varghese (1986)
<i>Cebidichthys violaceus</i> , Monkeyface eel	19	Fris and Horn (1993)
<i>Centropristis striata</i> , Black seabass	53	Shah Alam et al. (2008)
<i>Channa micropeltes</i> , Indonesian snakehead	52	Wee and Tacon (1982)
<i>C. punctatus</i> , Spotted snakehead	~47	Zehra and Khan (2012)
<i>C. striata</i> , Striped snakehead	55	Mohanty and Samantaray (1996)

(continued)

Table 2.2 (continued)

Species	Requirement, % dry matter	References	
<i>C. maculata</i> ♀ × <i>C. argus</i> ♂, Hybrid snakehead	51	Zhang et al. (2017b)	
<i>Chanos chanos</i> , Milkfish	~40	Jana et al. (2006)	
<i>Chelon ramada</i> , Thinlip grey mullet	24	Papaparaskeva-Papoutsoglou and Alexis (1986)	
<i>Cichlasoma urophthalmus</i> , Mexican mojarra	33	Martínez-Palacios et al. (1996)	
<i>Chirostoma estor</i> , Mexican (pike) silverside	41	Martínez-Palacios et al. (2007)	
<i>Cirrhinus mrigala</i> , Mrigal carp	32	Singh et al. (2008)	
<i>Clarias batrachus</i> , Walking catfish	40	Jindal (2011)	
<i>C. nieuhoftii</i> , Slender walking catfish	40	Kiriratnikom and Kiriratnikom (2012)	
<i>Coptodon zillii</i> , Redbelly tilapia	35	Mazid et al. (1979)	
<i>Ctenopharyngodon idella</i> , Grass carp	41–43	Dabrowski (1977)	
<i>Culter alburnus</i> , Topmouth culter	40	Zhang et al. (2016)	
<i>Cyprinus carpio</i> , Common carp	adult	25–50	Murai et al. (1985), Kaushik (1995) Nose (1979)
	Fry	43–47	
	Fingerling and grower	34–37	
	Adult	28–32	
<i>C. carpio</i> var. Jian, Jian carp	34.1	Liu et al. (2009)	
<i>Dacyllus aruanus</i> , Striped damsel	36	Vijayagopal et al. (2008)	
<i>Dicentrarchus labrax</i> , European seabass	32–56	Peres and Oliva-Teles (1999)	
<i>Diplodus vulgaris</i> , Two-banded seabream	35	Ozório et al. (2009)	
<i>Eleginops maclovinus</i> , Patagonian blennie	35	Sa et al. (2014)	
<i>Epinephelus akaara</i> , Red-spotted grouper	50.5	Wang et al. (2016)	
<i>E. coioides</i> , Orange-spotted grouper grow-out stage (~100 g) large size (275 g)	48.0	Luo et al. (2004)	
	46.7	Yan et al. (2020b)	
	43.8	Yan et al. (2020a)	
<i>E. fuscoguttatus</i> ♀ × <i>E. lanceolatus</i> ♂, Hybrid grouper	45–54	Jiang et al. (2015)	
<i>E. malabaricus</i> , Malabar grouper	42	Chen and Tsai (1994)	
<i>Gadus morhua</i> , Atlantic cod	~55	Pérez-Casanova et al. (2009)	
<i>G. morhua</i>	40–107 g	47–52	Árnason et al. (2010)
	400–900 g	36	
<i>Gobiocypris rarus</i> , Chinese rare minnow	35	Wu et al. (2016)	
<i>Hemibarbus maculatus</i> , Spotted barbel	35	Chen et al. (2010)	
<i>H. nemurus</i> , Asian redtail catfish	42	Khan et al. (1996)	

(continued)

Table 2.2 (continued)

Species	Requirement, % dry matter	References	
<i>H. wyckioides</i> , Asian red-tailed catfish	44	Deng et al. (2011)	
<i>Heteropneustes fossilis</i> , Stinging catfish	40	Khan and Abidi (2012)	
<i>Hippoglossus hippoglossus</i> , Atlantic halibut	48–62	Grisdale-Helland and Helland (1998)	
<i>Hypophthalmichthys nobilis</i> , Bighead carp	30	Santiago and Reyes (1991)	
<i>Ictalurus punctatus</i> , Channel catfish	24	Garling and Wilson (1976)	
<i>Ictiobus niger</i> , Black buffalo	41	Guy et al. (2018)	
<i>Labeo fimbriatus</i> , Fringed-lipped carp	26–27 (dp)	Jena et al. (2012)	
<i>L. rohita</i> , Rohu, roho labeo	30–40	Renukaradhya and Varghese (1986), Singh et al. (2005)	
<i>Liza haematocheila</i> , Redlip mullet	1-year 2-year	40–45 35	Yoshimatsu et al. (1992)
<i>L. ramada</i> , Thinlip grey mullet	24	Papaparaskeva-Papoutsoglou and Alexis (1986)	
<i>Lates calcarifer</i> , Asian seabass, barramundi	40–53	Bermudes et al. (2010)	
<i>Lepomis macrochirus</i> , Bluegill sunfish	42	Yang et al. (2016)	
<i>Lutjanus argentimaculatus</i> , Mangrove red snapper	40–43	Abbas et al. (2011)	
<i>Megalobrama terminalis</i> , Triangular bream	44	Yang et al. (2017)	
<i>Melanogrammus aeglefinus</i> , Haddock	~55	Kim and Lall (2001)	
<i>Metynnus hypsanchen</i> , Silver dollar	35	Singh et al. (2007)	
<i>Mugil cephalus</i> , Flathead grey mullet	30	De et al. (2012)	
<i>Nibea coibor</i> , Chu’s croaker	44–48	Huang et al. (2017)	
<i>Notemigonus crysoleucas</i> , Golden shiners	29	Lochmann and Phillips (1994)	
<i>Oncorhynchus mykiss</i> , Rainbow trout	24–35	Mahmud et al. (1996), Kim (1997)	
<i>Oplegnathus fasciatus</i> , Parrot fish	45	Kim et al. (2017)	
<i>Oreochromis aureus</i> , Blue tilapia	34	Winfree and Stickney (1981)	
<i>O. mossambicus</i> , Mozambique tilapia	40	Jauncey (1982)	
<i>O. niloticus</i> , Nile tilapia	29–40	Siddiqui et al. (1988), Kpundeh et al. (2015)	
<i>O. niloticus</i> , Genetically Improved Farmed Tilapia	29	Liu et al. (2017)	
<i>O. niloticus</i> × <i>O. aureus</i> , Hybrid tilapia	24	Shiau and Huang (1989)	
<i>Pampus argenteus</i> , Silver pomfret	49	Arshad Hossain et al. (2010)	
<i>Parachanna obscura</i> , Obscure snakehead	45–56	Kpoguet et al. (2013)	
<i>P. aestivalis</i> , Cortez flounder	47	González-Félix et al. (2014)	
<i>P. lethostigma</i> , Southern flounder	51	González et al. (2005)	

(continued)

Table 2.2 (continued)

Species	Requirement, % dry matter	References
<i>P. olivaceus</i> , Japanese or olive flounder	32–37 45–51	Kim et al. (2002) Lee et al. (2002)
<i>Piaractus mesopotamicus</i> (<i>Colossoma mitrei</i>), Pacu	35	Merola (1988)
<i>Platichthys stellatus</i> , Starry flounder	50	Lee et al. (2006)
<i>Pleuronectes platessa</i> , European plaice	70	In Oliva Teles et al. (2020)
<i>Poecilia reticulata</i> , Trinidad guppy	55	Kithsiri et al. (2010)
<i>Protonibea diacanthus</i> , Blackspotted croaker	49	Li et al. (2016)
<i>Pseudoplatystoma reticulatum</i> , Cachara catfish	49	Gomes Cornélio et al. (2014)
<i>Rhamdia quelen</i> , Black catfish	37	Salhi et al. (2004)
<i>Rutilus kutum</i> , Kutum	41.6	Ebrahimi and Ouraji (2012)
<i>Salmo salar</i> , Atlantic salmon smolt	58	Nordgarden et al. (2002)
<i>Sciaenops ocellatus</i> , Red drum	20–25 (db)	McGoogan and Gatlin (1998)
<i>Scophthalmus maximus</i> , Turbot	55–70	Liu et al. (2014), Caceres-Martinez et al. (1984)
<i>Sebastes schlegelii</i> , Rockfish	50	Cho et al. (2015)
<i>Seriola lalandi</i> , Yellowtail kingfish	63	Miegel et al. (2010)
<i>S. quinqueradiata</i> , Japanese yellowtail	38	Morimoto Kofuji et al. (2006)
<i>Siganus canaliculatus</i> , White-spotted spinefoot	36	Yousif et al. (1996)
<i>S. guttatus</i> , Goldlined spinefoot	30	Parazo (1990)
<i>S. rivulatus</i> , Spinefoot rabbitfish	~40	El-Dakar et al. (2011)
<i>Silurus asotus</i> , Amur catfish	45	Kim et al. (2014)
<i>Sinocyclocheilus grahami</i> , Dianchi golden-line barbell	~40	Deng et al. (2014)
<i>Sparus auratus</i> , Gilthead seabream	47	Ibarz et al. (2007)
<i>Sperata seenghala</i> , Giant river catfish	35	Ramzan Ali et al. (2014)
<i>Spinibarbus hollandi</i> , Taiwanese cyprinid	31	Yang et al. (2003)
<i>Symphysodon</i> spp., Discus	45–50	Chong et al. (2000)
<i>Takifugu obscurus</i> , Obscure puffer	42	Ye et al. (2017a)
<i>T. rubripes</i> , Tiger puffer	41	Kim and Lee (2009)
<i>Tor putitora</i> , Himalayan mahseer	40–45	Islam and Tanaka (2004)
<i>T. tambroides</i> , Malaysian mahseer	48	Ng et al. (2008)
<i>Totoaba macdonaldi</i> , Totoaba or totuava	~50	Minjarez-Osorio et al. (2012)
<i>Trachinotus carolinus</i> , Florida pompano	45	Lazo et al. (1998)
<i>Umbrina cirrosa</i> , Shi drum	51	Akpinar et al. (2012)

db digestible protein

^aTemperature dependent^bmg of digestible protein for maintenance per day per gram body mass

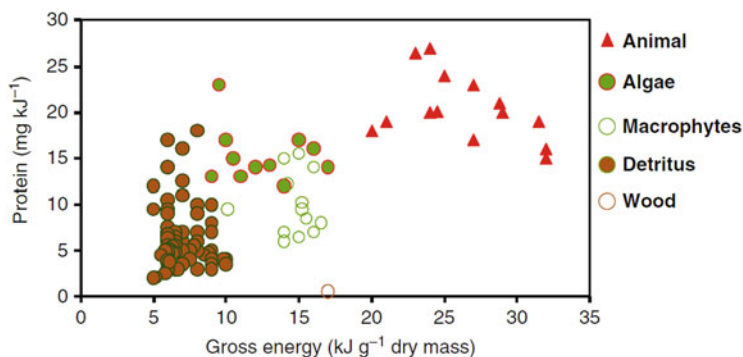


Fig. 2.1 Protein and gross energy in food resources available to aquatic consumers. (From German (2011) after Bowen et al. (1995), with permission from Elsevier)

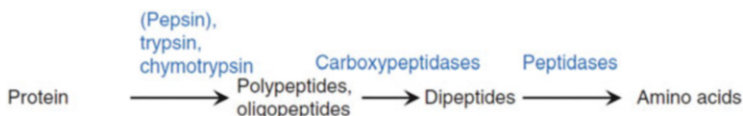


Fig. 2.2 Protein and the endogenous digestive enzymes fishes produce to hydrolyze them. The digestion of proteins requires multiple steps, beginning with initial hydrolysis in the lumen by extracellular enzymes and followed by membrane digestion by intestinal mucosal enzymes. The enzyme pepsin is listed in parentheses because agastric species (i.e., those that lack an acidic stomach) generally lack this. (From German (2011), with permission from Elsevier)

2.1 Requirement

Estimates of fish dietary protein requirements from many taxa are 2–4 times greater than the amount needed by other vertebrates (German 2011). Most fish species are carnivorous and are adapted to use protein as a preferred energy source over carbohydrate, and thus require high levels of dietary protein (20→70%: *Cebidichthys violaceus*→*Scophthalmus maximus*, *Pleuronectes platessa*) with an average of 42% (Oliva Teles et al. 2020). Figure 2.2 shows schematically the steps of protein digestion.

Some invertebrates appear to have lower protein requirements. The few papers, which studied protein requirement during the ontogenetic development, indicate that it decreases with increasing age (Table 2.2). In *Litopenaeus vannamei*, Smith et al. (1985) detected that the growth of small individuals is influenced more by protein level than protein source whereas growth of medium and large ones is more influenced by protein source than protein level. Various decapod crustaceans have a wide range of quantitative optimal dietary protein requirements strongly depending on the protein quality.

Early life stages of fishes can acquire exogenous proteinaceous nutrients as AAs or peptides, rather than intact proteins. In fact, the composition of the dietary proteins triggers life history traits. Nevertheless, even recent studies address gross protein requirements of fishes or aquatic invertebrates (Table 2.2) and continue to disclose that protein requirements follow an optimum dose-response curve.

Traditional in the experimental approach, Guy et al. (2018) evaluated the effects of dietary protein levels on growth and body composition of juveniles of the threatened omnivorous black buffalo (*Ictiobus niger*). Therefore, artificial propagation and culture are frequently a part of native species recovery plans, and developing formulated diets is a critical component of these plans. This study shows that a diet with 41% crude protein produces optimal growth for juvenile black buffalo.

Several data about protein requirement from different papers mutually agree well, others deviate considerably. Such discrepancies within one species are not astonishing, if one considers

- The high diversity of feed qualities applied (→Chap. 1, Hua and Bureau (2012))
- The missing standardization of larval age or developmental stages of juveniles used
- The feeding history of offspring and parental individuals (→AAN III “Nutritional Programming”)
- The genetic and epigenetic diversity within one species (→Chap. 40)

Abalone species are generally characterized by slow and heterogeneous growth rates. Therefore, artificial feed for abalone must contain sufficient protein and essential AAs (EAAs) in order to satisfy their nutrient requirements. To optimize aquaculture of the intrinsically herbivorous animals, artificial diets have to be amended with animal proteins. Bautista-Teruel et al. (2003) fed *Haliotis asinina* with fishmeal, shrimp meal, defatted soybean meal, and *Arthrospira* (*Spirulina*) sp. Highest weight gain (WG) is attained with a combination of fishmeal, shrimp meal, and defatted soybean meal. Astonishingly, abalone on pure plant protein diets (soybean, spirulina) shows lower WG than on mixed protein sources: The plant diets have relatively low methionine contents; therefore, the AA pattern is not appropriate and, obviously, the main reason for the low abalone growth on the pure plant diet.

Several papers demonstrate adverse effects in animals, if diets are deficient or in excess of proteins. Such effects are well documented in *Babylonia areolate*, *Eriocheir sinensis*, *Haliotis discus hannai*, *H. midae*, *H. iris*, *Jasus edwardsii*, *Penaeus monodon*, *Procambarus clarkia*, *Scylla serrata*, *Acipenser baerii* ♀ × *A. gueldenstaedtii* ♂, *Anguilla anguilla*, *Barbonymus altus*, *Gibelion catla*, *Diplodus vulgaris*, *Epinephelus malabaricus*, *Hippoglossus hippoglossus*, *Hypophthalmichthys nobilis*, *Labeo fimbriatus*, *L. rohita*, *Mystus nemurus*, *Oreochromis niloticus*, *Platichthys stellatus*, *Protonibea diacanthus*, *Barbonymus gonionotus*, *Scophthalmus maximus*, *Coptodon zillii*, or *Totoaba macdonaldi* (references in Table 2.2).

The mechanism by which excess of dietary protein adversely affects life history traits has to be discussed. Due to the limited capacity of digestive enzymes, excess dietary protein can be excreted as nitrogenous waste into the environment (Burford and Williams 2001). In an elaborate study, it has been demonstrated that particularly trypsin sets the physiological limit on growth rate and feed conversion (Torrisen et al. 1994; Lemieux et al. 1999). This is one of the classical modes of action.

In addition to limited trypsin capacity, hyperproteic diet proteins can cause oxidative damage on pancreas functions (Gu and Xu 2010) and acute hepatocellular injury in small mammals (Oarada et al. 2012). Furthermore, hyperproteic diet can reduce weight (Andriamihaja et al. 2010; Camiletti-Móiron et al. 2015). Whether this weight reduction is combined with oxidative stress is discussed controversially, since several studies report decreased internal oxidative stress upon hyperproteic diet (Lacroix et al. 2004; Machín et al. 2004). Therefore, more than one mechanism appears to be responsible for reduced growth or WG upon excess dietary protein supply. Illustrative biomolecular studies are sketched below.

Since many fishes are usually cultured outside their optimal temperature range, it is important to identify the nutritional requirements under these non-optimal thermal conditions. A few years ago, Bowyer et al. (2013) showed that the protein level can be reduced in diets for most marine species, but it is the quality and digestibility of nutrients in the diet that matters when fishes are cultured at non-optimal temperatures. At cooler temperatures, fish metabolism is reduced that, in turn, lowers the gut-transit time, digestibility, digestive enzyme activity and affects the uptake and absorption of nutrients required for energy and growth. Therefore, high-quality protein and low-lipid diets are necessary during cool-water periods.

In the same line of evidence, Oliva Teles et al. (2020) show in a meta-analysis that dietary protein requirements are directly related to fish trophic position and water salinity and slightly, but significantly inversely related to rearing temperature (Fig. 2.3).

Recent biomolecular studies shed some more light on underlying mechanisms of increased immunity. In juvenile big head carps, consumption of optimal dietary protein amounts improves liver immune responses (lysozyme, immunoglobulin heavy chain, alkaline phosphatase activity) (Sun et al. 2019). Transcriptome analysis identifies differentially expressed genes (DEGs) in the liver in response to different dietary protein levels, and bioinformatics links many DEGs to immune responses, inflammatory responses, and energy metabolism (Fig. 2.4). Moreover, abnormal serum biochemical indices are apparent in the high protein group, indicating that consuming excess protein aggravates liver metabolic burden.

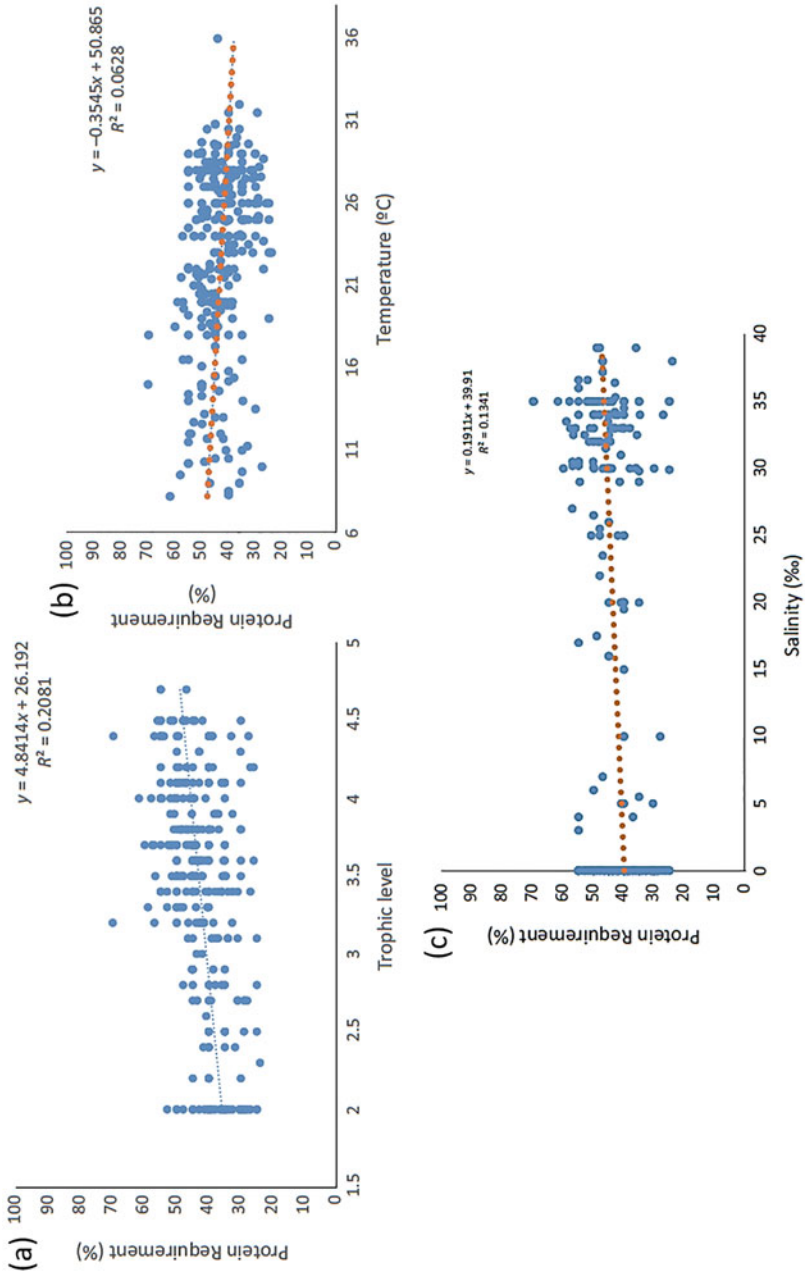


Fig. 2.3 Dietary protein requirement (%) of fishes as function of trophic levels (a), temperatures (b), and salinities (c). (From Oliva Teles et al. (2020), with permission from Wiley)

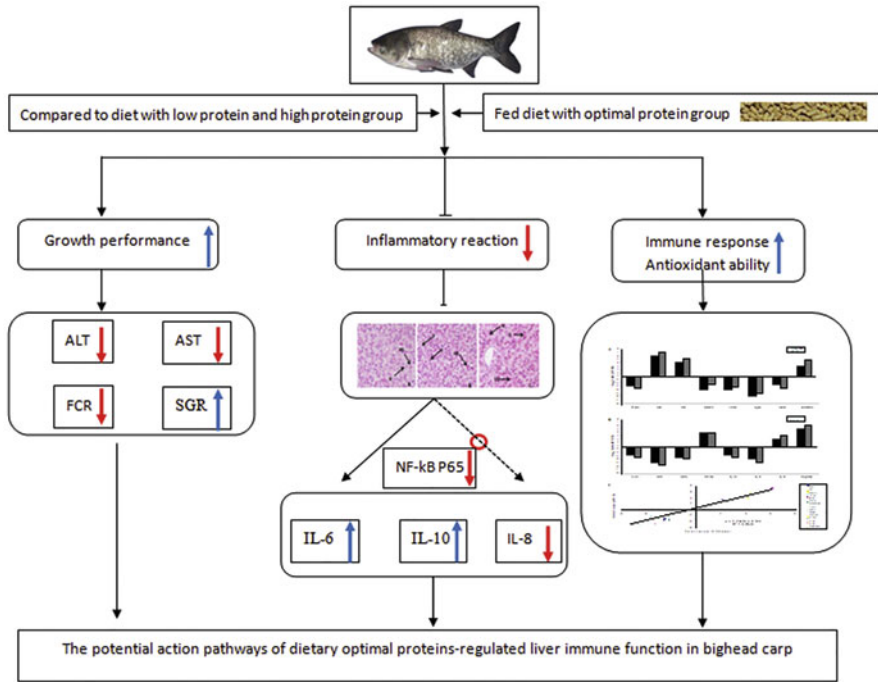


Fig. 2.4 Potential dietary protein-regulated pathways related to liver immune functions in juvenile bighead carp. *Blue* upregulated; *Red* downregulated. (From Sun et al. (2019), with permission from Elsevier)

Box 2.1 The Complement System

The complement system, also known as complement cascade, is a part of the immune system that enhances (complements) the ability of antibodies and phagocytic cells to clear microbes and damaged cells from an organism, promote inflammation, and attack the pathogen’s cell membrane. It is part of the innate immune system (Janeway et al. 2001), which is not adaptable and does not change during an individual’s lifetime. The complement system can be recruited and brought into action by antibodies generated by the adaptive immune system.

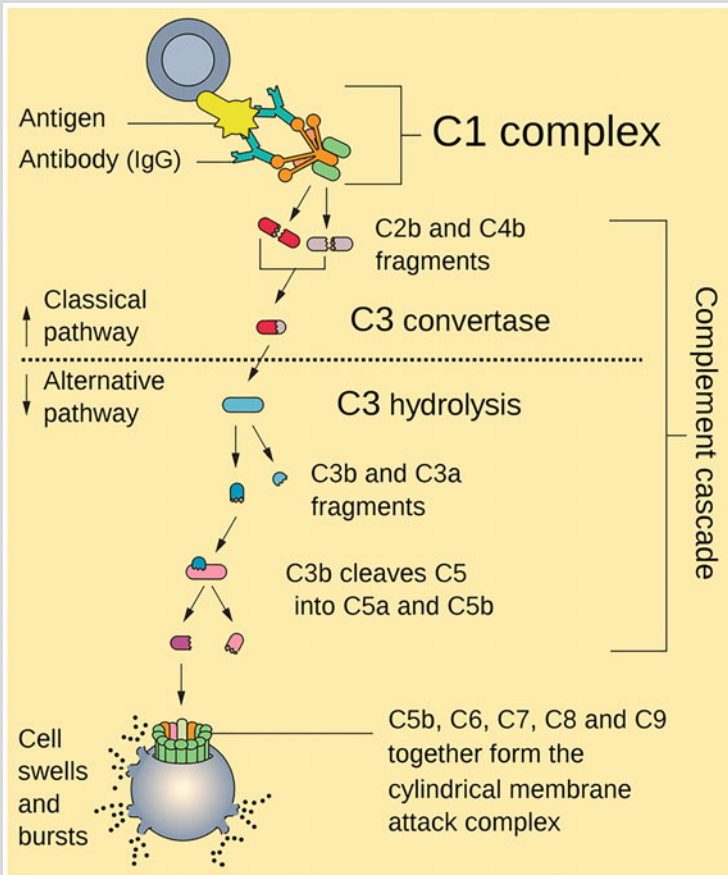
The complement system consists of a number of small proteins that are synthesized by the liver and circulate in the blood as inactive precursors. When stimulated by one of several triggers, proteases in the system cleave specific proteins to release cytokines and initiate an amplifying cascade of further cleavages. The result of this complement activation (or complement fixation cascade) is stimulation of phagocytes to clear foreign and damaged material, inflammation to attract additional phagocytes, and activation of the cell-killing membrane attack complex. Over 30 proteins and protein fragments make up

(continued)

Box 2.1 (continued)

the complement system, including serum proteins and cell membrane receptors.

In brief, three biochemical pathways activate the complement system: the classical complement pathway, the alternative complement pathway, and the lectin pathway (Ricklin et al. 2017) Box Fig. 1.



Box Fig. 1 Scheme of the complement system. The complement system is made up of about 30 proteins that work together to “complement” the action of antibodies in destroying bacteria. The term “complement” was coined by Nobel Laureate Paul Ehrlich (Chaplin 2005). Complement proteins circulate in the blood in an inactive form. When the first protein in the complement series is activated—typically by antibody that has locked onto an antigen—it sets in motion a domino effect. Each component takes its turn in a precise chain of steps known as the complement cascade. The product is a cylinder inserted into—and puncturing a hole in—the cell’s wall. With fluids and molecules flowing in and out, the cell swells and bursts (credit: DO11.10, Wikimedia)

The most closely linked metabolic pathways include glycolysis/gluconeogenesis, followed by pyruvate metabolism, the citrate cycle, and nitrogen metabolism. Some pathways associated with the immune system are also identified, including cell adhesion molecules, the PI3K-Akt signaling pathway,¹ complement and coagulation cascades, the Toll-like receptor signaling pathway,² and the NF- κ B signaling pathway. Many genes associated with the biosynthesis of immunity-related signaling pathways are detected in the LP vs. OP and HP vs. OP comparisons, including immune responses (lysozyme, immunoglobulin, alkaline phosphatase, etc.), inflammatory reactions (nuclear factor kappa B, interleukin-8, interleukin-10, etc.), and antioxidant ability (catalase, glutathione transferase, glutathione peroxidase, etc.). The discovery of immune-related pathways and unigenes provides one significant theoretical basis for understanding the molecular mechanisms of dietary protein regulation of liver function.

In one invertebrate equivalent *Macrobrachium nipponense*, Lv et al. (2021) showed that the interaction of dietary protein supply and rearing temperature affects alanine aminotransferase (ALT) and complement component 4 (C4). In contrast to bighead carp, immunity of this shrimp does not significantly improve solely due to modulation of dietary protein contents. In a marine counterpart, Ma et al. (2020) identified that deficient or excessive dietary protein levels depress the growth, health, and anti-stress capacity of abalone (*H. discus hannai*). 17.6% or 43.3% (but 30%, Table 2.2) of dietary protein contents are not recommended (Fig. 2.5): on non-appropriate diet, pro-inflammatory cytokine *tnf- α* is upregulated (Fig. 2.5a), and *nrf2*, a major transcription factor of cytoprotective responses to oxidative stress is downregulated (Fig. 2.5b). Consequently, animals are increasingly susceptible to heat stress (Fig. 2.5c).

2.2 Amino Acid Landscapes

Proteins differ from each another. It can easily be predicted that different AA patterns (“landscapes”) translate into higher trophic levels along the food chain. Consequently, a central challenge is to understand how alterations of community structure transmit into food web processes (Hooper et al. 2005). Herein, macroinvertebrates are a critical trophic link between basal energy sources and higher-order consumers. If macroinvertebrate taxa differ in the quality and quantity

¹Intracellular signaling pathway is important in regulating the cell cycle, directly related to cellular quiescence, proliferation, cancer, and longevity. PI3K activation phosphorylates and activates AKT (protein kinase B), localizing it in the plasma membrane (King et al. 2015).

²Toll-like receptor signaling pathways play crucial roles in the innate immune system by recognizing pathogen-associated molecular patterns derived from various microbes. Toll-like receptors signal through the recruitment of specific adaptor molecules, leading to activation of the transcription factors NF- κ B and IRFs, which dictate the outcome of innate immune responses (Kawasaki and Kawai 2014).

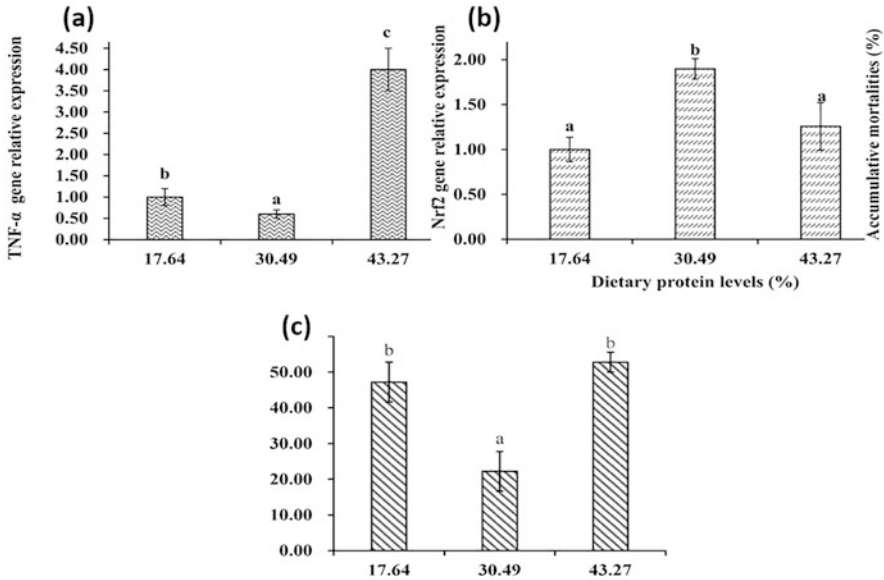


Fig. 2.5 Expressions of the immune-related genes (*tnf- α* (a) and *nrf2* (b)) in the hepatopancreas and accumulative mortalities (c) of abalone *H. discus hannai* after the heat challenge test. Abalones were fed diets with different protein levels. All data are mean \pm SE of three replicates. Different letters indicate significant differences ($P < 0.05$). (From Ma et al. (2020), with permission from Elsevier)

of nutrients they contain, then alteration of macroinvertebrate community composition will affect predator fitness (Dwyer et al. 2018). These authors showed that AA composition vary significantly among taxa; simulated deterioration of macroinvertebrate communities changes the AA landscape, resulting in lower availability of essential AAs, particularly threonine, phenylalanine, proline, and tyrosine to carnivores.

In a succeeding paper, Dwyer et al. (2020) verified that changes in AA landscapes affect the growth of individuals of higher trophic levels and the success of these populations. They determined whether AA composition of animal prey alone affects protein synthesis efficiency and N wastage of a freshwater carnivore. River blackfish (*Gadopsis marmoratus*) were fed two diets differing only in AA composition: the first diet matches the composition of the fish themselves, representing a balanced “ideal protein,” whereas the second diet matches the composition of a major prey (*Macrobrachium australiense*). By measuring the postprandial increase in metabolic rate and ammonia excretion, it turns out that the AA composition of the fish diet is associated with an increase in protein synthesis, whereas the shrimp diet doubles the amount of dietary AAs directed to catabolic energy production and N wastage.

In a subsequent study, Shakya et al. (2021) show that the AA profile of freshwater macroinvertebrates is not only taxon-specific but can vary temporally (between seasons) and spatially between sites depending on taxa. A change in the community

composition of macroinvertebrates can therefore potentially alter the nutritional landscape available to higher-order consumers within riverine environments. How the influence of seasonal and spatial variation in AAs due to inter- and intraspecies differences translates into the growth and metabolism of top predators and across the food web deserves future studies and may be almost as significant as the biochemical bottom-up effect of dietary polyunsaturated fatty acids (→Chap. 30). Therefore, in the following chapters, the controlling effects of individual AAs in aquafeeds will be demonstrated.

2.3 Nutrient-Specific Foraging

How does an animal identify which macronutrients are essential and which may have been deficient in previous feedings? Furthermore, how does it understand or feel that compensatory feeding is overdue? This is an ultimate goal in nutritional ecology.

In nature, many herbivores and omnivores adjust their food selection behavior to regulate the intake of multiple nutrients. Carnivores, however, are generally assumed to optimize the rate of prey capture rather than select prey according to nutrient composition. In an intriguing study, however, Mayntz et al. (2005) showed experimentally that invertebrate predators can forage selectively for protein and lipids to redress specific nutritional imbalances. This selection can take place at different stages of prey handling: The predator may select among foods of different nutritional composition, eat more of a prey if it is rich in nutrients that the predator is deficient in, or extract specific nutrients from a single prey item. This applies particularly to an environment where there is a high probability of encountering nutritionally heterogeneous foods.

There is a growing awareness that nutritional phenotypes are best understood in a multidimensional context, where foraging is viewed as a process of balancing the intake and use of multiple nutrients to satisfy complex and dynamic nutrient needs (Raubenheimer et al. 2009). Simpson and Raubenheimer (1993) coined the term “geometry of nutritional decisions” of an animal, and Mayntz et al. (2005), for instance, reported about nutrient-specific foraging in invertebrate predators.

In details, a common approach has been to assume that a single component dominates these interactions, with the focus usually on energy, nitrogen, or allelochemicals. However, a substantial body of data exists for a number of systems showing that this simplification is not in general warranted because consumer–food relations are usually dominated by the simultaneous effects of several dietary components. Numerous laboratory studies have shown that this view can yield novel insights into unresolved questions and provide a framework for generating new hypotheses (Raubenheimer 2011). Comparably controlled conditions as in laboratory studies do also exist in aquaculture so that this approach is feasible for application in this discipline, since it has already been successfully applied to companion animals (Raubenheimer et al. 2015). Raubenheimer (2011) proposed mixture triangles, which enable an n -dimensional problem to be visualized in an $n-1$

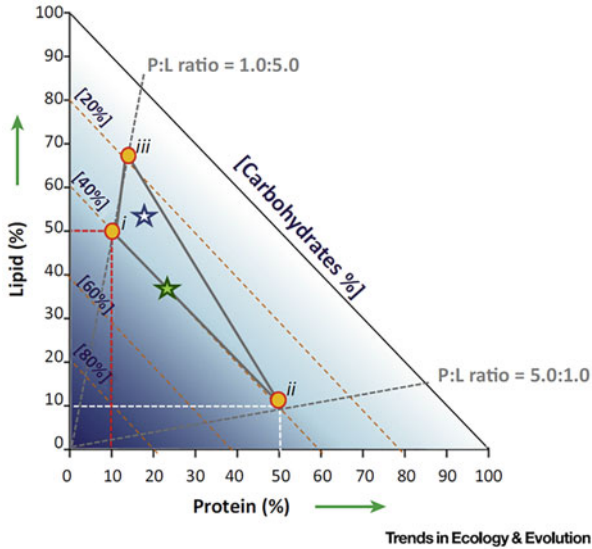


Fig. 2.6 Right-Angled Mixture Triangles (RMTs) provide a platform to plot three components in 2D graphs using proportional data (Raubenheimer et al. 2009). Here Machovsky-Capuska et al. (2016b) model foods, each with a different mixture of protein (%P), lipid (%L), and carbohydrate (%C). Carbohydrate concentration increases with density of blue shading (i.e., across the negative diagonal carbohydrate isolines). Hypothetical food **i** contains 10% P, 50% L, and 40% C, whereas food **ii** contains 50% P, 10% L, and 40% C. The model also illustrates that if an animal mixes its intake of two foods (e.g., **i** and **ii**), the resulting diet composition is constrained to lie on the line connecting the foods (e.g., green star). By mixing its intake of three foods (e.g., **i**, **ii**, and **s**), the accessible space expands to a triangle connecting these foods (e.g., blue star). (From Machovsky-Capuska et al. (2016b), with permission from Elsevier)

dimensional space. A recently developed tool from nutritional geometry is the Right-Angled Mixture Triangle (RMT) (Fig. 2.6). Each point represents a mixture of protein (P), lipid (L), and carbohydrate (C). %P and %L increase along the x- and y-axes, respectively, and the P:L ratio of a mixture is given by the slope of the radial that connects the point to the origin. %C of a point is determined as the difference between 100% and the value at which a negatively sloped diagonal through the point intersects with the two axes (Fig. 2.6).

The application of RMTs is shown in a recent example. To understand the nutritional requirements of species and predict their response to environmental changes, Rowe et al. (2018) combined nutritional geometry and metabolic performance. The authors provide evidence that the Indo-Pacific damselfishes (*Abudefduf vaigiensis*) adjust their energy intake and select specific macronutrients in their diets, thereby reducing the effects of important environmental conditions such as thermal variation on critical metrics of performance when stressed.

In particular, the proportional macronutrient intakes by *A. vaigiensis* in different diet and temperature treatments are shown in Fig. 2.7, together with the macronutrient composition of the experimental foods and an estimate of the natural diet. A first point to note is that the fishes feed non-randomly. This is evident in Fig. 2.7 as

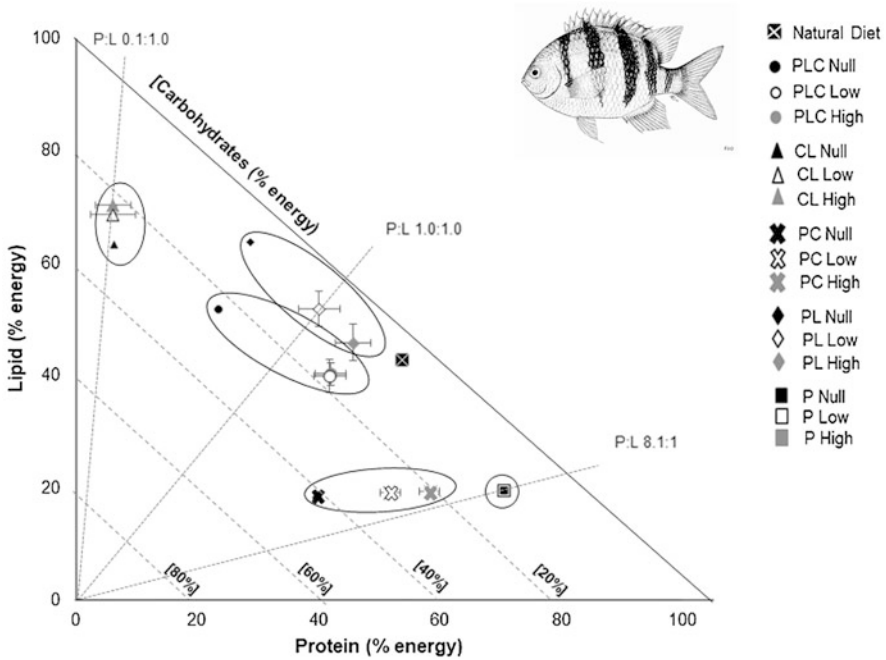


Fig. 2.7 Right-Angled Mixture Triangle showing foraging choices of damselfish. Each diet represents a proportional mixture of protein (P), lipid (L) and carbohydrate (C) (by energy). To geometrically define diets in an RMT, % P is plotted against % L. Considering that the three macronutrients in the mixture sum to 100%, plotting % P (first axis) and % L (second axis) will automatically reflect the value of % C in the third axis (Raubenheimer 2011). Diets are presented as mean (\pm SE) for each free choice (PLC) and restricted treatments (CL, PC, and PL) and compared with a null hypothesis that damselfish consume equal proportions of foods (solid black) at low (hollow black) and high temperatures (solid grey). Rowe et al. (2018) also included in the RMT the 98% energetic dietary intake (black square with white cross) of *A. vaigiensis* in the wild (estimated from Fr  d  rich et al. (2009)). The grey dotted lines given by the slope of the radial that connects the point to the origin represent the P:L ratios of the highest and lowest P:L treatments offered. (From Rowe et al. (2018), with permission from Springer Nature; image credit FAO)

the proportions of macronutrients eaten by fishes differed from the null hypothesis that *A. vaigiensis* consume equal proportions of foods.

There is considerable spread in macronutrient intake because of the different nutritional treatments, and there is a strong effect of temperature, but it varied depending on the treatment (Fig. 2.7). Specifically, high temperatures increase the proportional energy intake on the different nutritional treatments. The animals tend to adjust the macronutrient intake closer to their natural diet, especially by increasing protein consumption in the high-temperature treatment (Fig. 2.7). Such nutrient-specific diet selection is consistent with the ecology of marine organisms, which forage in nutritionally complex and fluctuating marine environments that vary spatially and temporally (Tait et al. 2014; Machovsky-Capuska et al. 2016a, 2018).

In nature, dietary choices can have profound effects on growth, survival, and reproduction, and the mechanisms that determine what fish choose to eat have been

strongly molded by natural selection. Fish bring these mechanisms with them into culture, where they can cause problems, in terms of production, welfare, and environmental impact (Raubenheimer et al. 2012). Long-established cultured species that are farmed intensively, such as salmonids, are usually provided with feeds formulated to contain sufficient nutrients to meet all their known requirements. In theory, fish cultured in this way have neither the need nor the opportunity to be selective about their food. However, there are reasons why an ideal situation is rarely achieved. In the first place, even for well-established species, knowledge about requirements is incomplete. Second, devising optimal feeds for fish of all ages raised in different environments (with respect to temperature, light regimes, and water quality, for example) and that differ in status with respect to maturation, and disease may simply not be possible. In addition, the capacity to provide what is known to be ideal may be compromised by problems of the sustainable supply of potential feed ingredients. For all these reasons, cultured fish may well be given food that is imperfect, with the feed formulation representing a compromise involving nutritional requirements, processing and economic and environmental constraints (Raubenheimer et al. (2012) and references therein). Choosing to feed on smaller conspecifics is a natural aspect of diet selection and a means to overcome protein deficiencies, since smaller conspecifics represent high-quality prey for piscivores, at least in terms of provision of all nutrients needed for growth; cannibalism is therefore a natural feeding strategy in some fishes that are cultured (Jobling et al. 2012). Moreover, elevated cannibalism in farmed carnivores should be considered as inappropriate provision of proteinaceous feeds.

2.4 Concluding Remarks

There is an increasing catalog of studies figuring out the dietary protein requirement in farmed aquatic animals. It is obvious that proteins are significant nutrients and energy sources. However, most approaches follow the traditional format of production studies: feeding → weighing → calculating losses by excretion. Since most often the protein sources vary, the resulting productive traits become almost incomparable. This concern applies to studies of most macro- and micronutrients and is an immanent weakness of studies of productive traits. Furthermore, interactions of macronutrients and their influence on protein requirements are well documented from ecological studies, but considered rather scarcely in aquaculture. It can be predicted that the application of the sketched RMT approach has the potential to improve aquafeeds' quality. Moreover, in the age of highly developed biomolecular and bioinformatics techniques, the weakness of the classical aquaculture production approach has to be overcome. In brief:

- The studied strains of aquatic species have to be characterized including hints of potential specific life history traits as discussed in depth in Chap. 40. This information should be deposited in central aquaculture data base.

- The effect of proteinaceous nutrients on various traits has to be traced back to the “omics” levels to identify general regulatory pathways and to provide a means to translate from studied population to the other one and from one species to the other one. One encouraging example is shown above with the affected immunity traits in bighead carp.
- Feedback mechanisms of the intestinal microbiota have to be elucidated.
- Of particular interest is further the identification of biomolecular (genetic, epigenetic) pathways of excess nutrition: Which traits are affected when aquatic animals are fed proteinaceous feeds in excess, and how does this interact with other macro- and micronutrients?
- Almost all papers neglect the circadian rhythmicity of the animals. They consider creatures more or less as simple cybernetic systems. However, in AAN I “Chrononutrition” (Steinberg 2018), we have seen that all animals studied so far, from invertebrates up to mammals, are subject to a circadian rhythmicity with distinct ups and lows of metabolic activity. The unstudied aquatic animals are no exception to this rule.

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