J Appl Phycol
DOI 10.1007/s10811-007-9290-4

Seaweeds preferred by herbivorous fishes

G. Tolentino-Pablico · N. Bailly · R. Froese · C. Elloran

Received: 21 April 2007 / Revised and Accepted: 5 November 2007

Abstract Marine macrobenthic algae (or seaweeds), epiphytic microalgae, and other aquatic plants constitute the main food items of marine herbivorous fishes. About 5% of all fish species are herbivorous; only 30% of these are marine, most of them living in coral reefs. An analysis was performed on all the seaweeds that formed part of the natural diet of these fishes, based on information contained in FishBase (http://www.fishbase.org). The results showed that many coral-reef-associated marine herbivorous fishes, such as the families Blennidae, Kyphosidae and Siganidae, fed selectively on filamentous and turf fleshy seaweeds, which they prefer over calcareous coralline and encrusting species. In particular, Chlorophyceae of the genera *Cladophora*, *Enteromorpha* and *Ulva* were preferred by *Scartichthys viridis* (Blennidae), *Girella* spp. (Kyphosidae), *Sarpa salpa* (Sparidae), and Phaeophyceae in the genera *Sargassum* and *Dictyota* were preferred by *Kyphosus* spp. (Kyphosidae) and *Siganus* spp. (Siganidae). A web-based tool was developed to provide information on plants (algae, seagrasses, terrestrial plants and fruits) preferred as food by herbivorous fishes (http://www.incofish.org/herbitool.php). The tool is intended to assist aquaculturists, conservationists and ecosystem-based fisheries managers.

Keywords Aquaculture · Diet composition · FishBase · Food items · Herbivores tool

G. Tolentino-Pablico (✉) · N. Bailly · C. Elloran
Philippine Office / Natural Resource Management,
WorldFish Center,
Khush Hall, IRRI College, Los Baños,
Laguna 4031, Philippines
e-mail: g.pablico@cgiar.org

N. Bailly
e-mail: n.bailly@cgiar.org

C. Elloran
e-mail: c.elloran@cgiar.org

R. Froese
Leibniz-Institut für Meereswissenschaften IfM-GEOMAR,
Düsternbrooker Weg 20,
24105 Kiel, Germany
e-mail: rfroese@ifm-geomar.de

Introduction

Filamentous and turf seaweeds, Bacillariophyta, Dinophyceae, Cyanobacteria, associated meiofauna and detritus are food resources for grazing herbivorous fishes (Ojeda and Muñoz 1999; Crossman et al. 2001; Choat et al. 2002) and form a complex assemblage called the epilithic algal matrix (EAM) (Wilson et al. 2003). The bulk of the diet consists mainly of turf and filamentous algae, and macrophytes, but a small amount of animal materials may be ingested (Horn et al. 1982); other food items ingested are detritus or "unidentified organic matter". Wilson et al. (2003) have even suggested that fishes assimilate more detritus than algae and should be considered as detritivores.

The susceptibility of algae to grazing by herbivorous fishes depends on algal morphology (Hay 1984; Lewis 1985; Hay 1997). Most herbivorous fishes prefer fleshy seaweeds over calcareous coralline and encrusting seaweeds (Montgomery and Gerking 1980; Horn et al. 1982; Ojeda and Muñoz 1999). This preference appears to have developed from the temporal and spatial variation in food availability (Horn et al. 1982, 1986; Andrew and Jones 1990; Jones and Andrew 1990); the presence or absence of secondary metabolites produced as chemical defenses against herbivory (Lewis 1985; Steinberg 1986; Duffy and Paul 1992; Cronin and Hay 1996; Cronin et al. 1997; Hay 1997; Cetrulo and Hay 2000; Erickson et al. 2006); and by

nutritional qualities in terms of energy, micro-nutrient, calorie and protein content (Montgomery and Gerking 1980; Edwards and Horn 1982; Neighbors and Horn 1991; Pillans et al. 2004).

The objectives of this paper are (1) to identify the dominant seaweed groups among the Florideophyceae, Chlorophyceae and Phaeophyceae that are ingested by herbivorous fish, and (2) to develop a web-based tool for identifying the food preferences of herbivorous fishes by country, FAO area or ecosystem. This would also provide knowledge on the distribution and diversity of herbivorous fishes in different localities and ecosystems around the world. The eventual goal is to provide a tool for natural resource managers involved in aquaculture, fisheries, and conservation of marine herbivorous fishes.

Materials and methods

Seaweeds as food

The name "fish" refers to non-Tetrapoda Vertebrata species. Larvae were not included in the study. "Herbivorous fishes" or "herbivores" refer to adults and juveniles of fish species with trophic levels between 2.0 to 2.2. Trophic levels were estimated (1) from diet composition data, covering the whole range of food items consumed by a given species at a given locality and season, and (2) from food items studies, if no information on diet was available (Pauly and Sa-a 2000).

In FishBase, food items of fishes were classified into 58 categories, defined as functional groups of taxa that shared the same consumers and resources within a food web (Sa-a et al. 2000). The food items and diet data were drawn from peer-reviewed publications, theses and dissertations that contained lists of seaweed species that have been found in the stomach or otherwise known to be ingested by a given fish.

An analysis was performed on the seaweeds that formed part of the natural diet and stomach contents of herbivorous fishes, based on information contained in FishBase. Seaweeds consumed by a given species were grouped by phylum and by family; the taxonomy and validity of algal names were verified using AlgaeBase (Guiry and Guiry 2007; http://www.algaebase.org).

Herbivorous fish tool

The web-based tool available in the Incofish website was developed to retrieve information on herbivorous fishes from FishBase (Fig. 1). The tool was developed using open source resources such as PHP Hypertext Preprocessor (PHP), Hypertext Markup Language (HTML), Cascading Style Sheet (CSS) and MySQL for the backend database.

Results

Seaweeds as food

Herbivorous fishes accounted for only 5% (1,660/29,500) of the total number of fish species known globally. Of this quantity, 89% are from tropical waters (1,441/1,660) while 3% are temperate species (49/1,660).

Seventy percent, 28% and 2% are freshwater, marine, and brackishwater species, respectively (Froese and Pauly 2007).

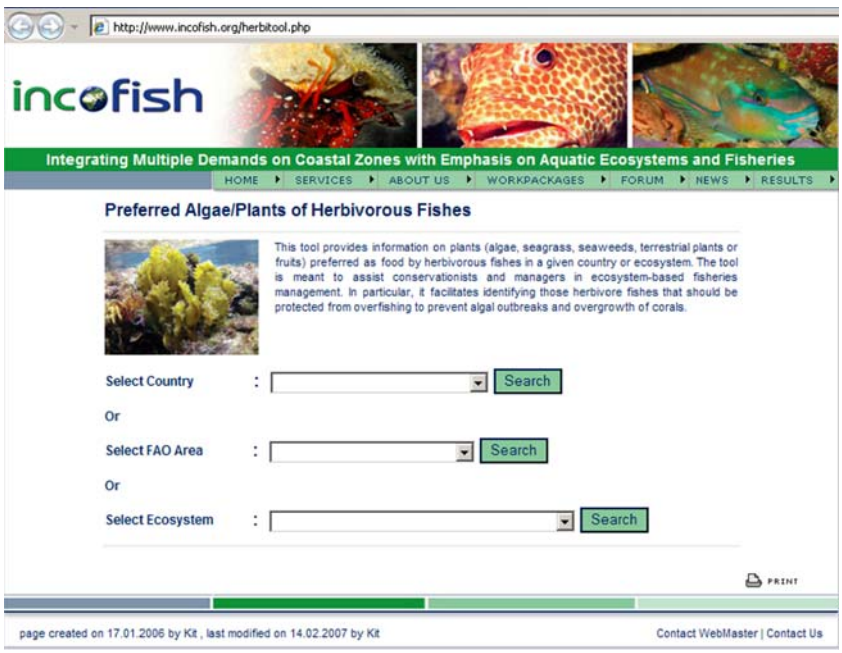

Fig. 1 The search page of the herbivorous fish tool, http://www.incofish.org/herbitool.php

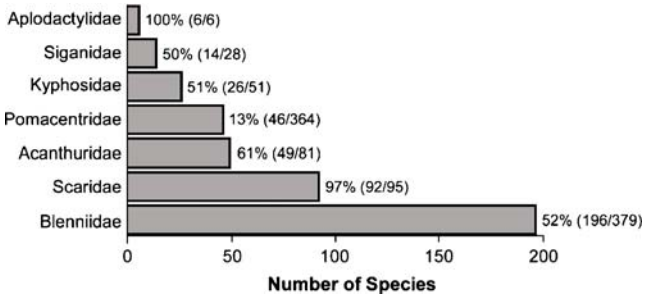

Fig. 2 Number of species and percentage of marine herbivorous fishes per family

The marine herbivores were mainly in coral-reef-associated areas while others were demersal or benthopelagic.

Families with the most representatives of herbivorous species are shown in Fig. 2. The following families had the most representatives of marine herbivores: Blenniidae (combtooth blennies), Scaridae (parrotfishes), Acanthuridae (surgeonfishes), Pomacentridae (damselfishes), Kyphosidae (sea chubs), Siganidae (rabbitfishes) and Aplodactylidae (marblefishes). These families represent the greatest number of species of marine herbivorous fishes in coral reefs, with Acanthuridae and Scaridae being the most abundant.

The total numbers of all seaweed species consumed by fishes reported in FishBase are shown in Table 1. The numbers exclude any unidentified seaweeds species recorded. Class Florideophyceae was the most often reported component of herbivore diets, followed by the class Phaeophyceae, dominated by families Dictyotaceae and Sargassaceae, and class Chlorophyceae, recorded mainly from the family Ulvaceae.

The seaweed higher taxa most often ingested by herviborous fishes are shown in Table 2. In class Florideophyceae, the genera *Ceramium*, *Corallina*, *Jania*, *Gelidium*, *Laurencia*, and *Polysiphonia* were ingested mainly by *Sarpa*, *Scartichthys*, *Hermosilla*, *Girella* spp. and *Siganus* spp.; in Phaeophyceae, the genera *Dictyota* and *Sargassum* were ingested mainly by *Acanthurus*, *Naso*, *Kyphosus*, *Holacanthus*, *Amphiprion* and *Sarpa* spp. In addition, the fleshy and filamentous members of the Chlorophyceae, such as *Ulva*, *Enteromorpha* and *Cladophora* were also ingested by some of these fishes.

A comparison of the number of species of each class Florideophyceae, Phaeophyceae and Chlorophyceae ingested by marine herbivorous fishes is shown in Fig. 3. Kyphosidae, with mostly benthopelagic species, consumed the highest number of Florideophyceae. Among the other families, where species were mostly coral-reef-associated, only Acanthuridae ingested a higher number of Chlorophyceae. Marine benthic algae were preferred mainly by members of the acanthurids, blenniids, kyphosids and siganids. These herbivores were nearly always reef-associated species, except for families Kyphosidae and Blenniidae, which were benthopelagic and demersal, respectively.

Table 1 Total numbers of seaweed families and species ingested by herbivorous fishes recorded in FishBase

	Number of families	Number of species
Florideophyceae	33	145
Phaeophyceae	20	81
Chlorophyceae	14	33

Table 2 Dominant seaweeds consumed by herbivorous fishes

Frequently ingested seaweeds		Herbivorous fish
Florideophyceae:		
Ceramiaceae	*Ceramium*	*Sarpa salpa*
Corallinaceae	*Corallina*	*Scartichthys* spp.
	Jania	*Hermosilla azurea*
Gelidiaceae	*Gelidium*	*Girella* spp.
Rhodomelaceae	*Laurencia*	*Siganus* spp.
	Polysiphonia	
Phaeophyceae:		
Sargassaceae	*Sargassum*	*Acanthurus* spp.
		Naso spp.
		Kyphosus spp.
Dictyotaceae	*Dictyota*	*Holacanthus passer*
		Amphiprion spp.
		Sarpa salpa
Chlorophyceae:		
Ulvaceae	*Ulva,*	*Girella* spp.
	Enteromorpha	*Sarpa salpa*
Cladophoraceae	*Cladophora*	*Scartichthys viridis*
		Liza vaigiensis

Herbivorous fish tool

This tool provides information on plants (algae, seagrasses, terrestrial plants or fruits) preferred as food by adults and juveniles of herbivorous fishes. Lists of herbivorous fishes are created if searched by country, FAO area or ecosystem. It provides the fish common names, maximum length, trophic level, general aquaculture use, climate zone and diet. Selecting a species opens its species summary page in FishBase, which provides information on its taxonomy, distribution, biological and environmental characteristics,

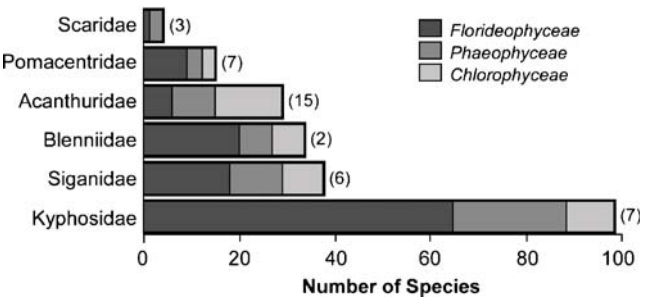

Fig. 3 Number of seaweed species consumed by fishes recorded in FishBase. Numbers of herbivores examined are in parentheses

and other topics and links. Selecting the trophic level of a given species opens a report showing the list of its preferred algae/plants, and identifies the algal food group or its taxonomic classification. The algal scientific names are linked to AlgaeBase. Selecting the "Diet" button of herbivorous fish will show up the species' diet composition, which is based on studies in percent weight or volume reported for a sample. The unavailability of information on food items and diet composition of some herbivores illustrates the research gaps.

Discussion

Seaweeds as food

The analysis of food items and diets from published references indicates the expected diversity of feeding modes in herbivorous fishes through ontogeny. The larval and post-larval stages of most herbivorous fishes are planktivorous, progressively becoming omnivorous during their juvenile stages, and then herbivorous upon reaching maturity (Benavides et al. 1994). A shift from animal to plant diet is related to an increase in the capability of assimilating the walls of seaweed and plant cells as the length of the digestive tract increases during ontogeny (Horn 1989; Clements and Choat 1993; Benavides et al. 1994). Many herbivorous fishes have the low stomach pH levels and specialized guts required for the digestion of plant materials (Horn and Messer 1992).

Higher temperatures facilitate plant material digestion when cooler temperatures may not allow herbivorous fishes to process enough food material to meet their metabolic demands (Floeter et al. 2005). Hence, temperature-related feeding and digestive processes are most likely the principal inducers of geographical distribution patterns. Accordingly, as shown from studies compiled in FishBase, these fishes are more abundant at lower than higher latitudes, especially in coral reef areas, where they present high species diversity and biomass. The herbivorous fishes are thus the major component of the coral reef ecosystems balancing seaweed production, whereas sea-urchins, gastropods and crustaceans perform this function in temperate waters. Moreover, fish herbivory often induces adaptations of seaweed morphology, structure, and biochemistry to resist grazing (Hay 1997).

Knowledge on herbivorous fishes and their food items is thus important in the design and management of marine protected areas, e.g., avoid seaweed overgrowth and outbreaks.

Montgomery and Gerking (1980) found that Chlorophyceae were superior to Phaeophyceae, and Phaeophyceae superior to Florideophyceae in terms of caloric and nutrient contents. Some studies have shown the importance of toughness and calcification as feeding deterrents. Moreover, Paul and Hay (1986) found that many tough calcified seaweeds produce unusual secondary metabolites that could act as chemical defenses and thus lead to low susceptibility to herbivory. Accordingly, in FishBase, most of the dominant Chlorohyceae and Phaeophyceae ingested by herbivorous fishes possess fleshy filamentous and leathery foliose thalli possessing alleged morphological and/or secondary compounds that are highly susceptible to fish grazing (Lewis 1985). Hay (1984) also reported that some Phaeophyceae that produce polyphenolics or phenolic acids, were consumed at high intermediate rates, suggesting that these secondary compounds were not effective deterrents for some herbivorous fishes. In addition, turf filamentous and branching Florideophyceae, such as *Ceramium*, *Polysiphonia* and *Gelidium*, were the major food items of many reef-associated species. For instance, the diet of *Scartichthys viridis* individuals less than 13 cm total length consisted of the foliose Chlorophyceae, *Ulva* and *Enteromorpha*, but when it reached over 22 cm total length, the tough Florideophyceae *Gelidium* comprised the bulk of the gut contents (Muñoz and Ojeda 2000). Ochavillo et al. (1992) also reported that turf algae were the major component of the diet of Scaridae. In addition, large fishes such as *Hermosilla*, *Girella* and *Sarpa* frequently ingest crustose and coralline seaweeds such as *Corallina*, *Jania* and *Gelidiella*.

Crossman et al. (2001) have demonstrated that detritus from EAM is high in protein amino acids and of potential food value for grazing fishes. Diet composition studies of some species of acanthurids and scarids recorded as herbivorous in FishBase showed that at least 50% of the diet was composed of detritus. Many of the coral reef fishes selectively feed on detritus and this represents a major dietary constituent (Wilson et al. 2003). Gut segments of detritivorous scarids and acanthurids had significantly higher total amino acid concentrations than planktivores and omnivores, with algivores being the lowest (Crossman et al. 2005). Nevertheless, the relative length of the gut of the species with trophic levels between 2.0 and 2.2 should be explored since it might indicate the importance of plant material assimilation (Horn and Messer 1992).

Herbivorous fish tool

The herbivorous fish tool was developed to provide information on biological data, taxonomy, distribution and dominant algal food. This decision support tool is intended to assist fish farming, ecosystem-based fishery management, and conservation domains.

A compilation of the different algal/plant food items of a fish species can be used to identify food preferences in herbivorous fishes for which detailed diet composition data are not available, and in preliminary estimates of trophic

levels (Sa-a et al. 2000). It facilitates identification of those herbivorous fishes that should be protected from overfishing to prevent algal outbreaks in coral reefs and other tropical areas. Knowledge of the diet of herbivorous fish in terms of species and nutrient content is important to improve their aquaculture by delivering the most efficient food.

A next step could be to create a "Detritivores tool" and link it to the "Herbivores tool" when the corresponding herbivory/detritivory part of the diet is elucidated.

Summary and recommendations

Seaweeds have been shown to be a source of minerals and nutrients in fish diets and the main food for many herbivorous fishes. Some seaweed characteristics have important direct and indirect effects on seaweed–herbivorous fish interactions. The presence of chemical deterrents, as well as the morphological and nutritional characteristics of some seaweed species may prevent intense feeding by herbivorous fishes. Defended seaweeds become safe sites for small and less mobile invertebrates, and habitats for larvae and juveniles fishes. On the other hand, if the seaweeds are not removed by herbivorous fishes, they could become competitively dominant organisms and may eventually destroy the coral reefs. The exploitation of these areas must be well-managed.

Developing herbivorous fish aquaculture in tropical developing countries is a pro-poor alternative to carnivorous fish aquaculture, which usually requires fish in the feeds. This means more pressure on the already globally depleted fish stocks, and a protein-rich diet is usually the most expensive component of aquaculture. This could hamper further growth of farms, especially in poor areas, for subsistence food. The less costly approach is to provide herbivorous fishes with algal supplements and natural periphyton in ponds (Keshavanath et al. 2002). The availability and abundant year-end supply of seaweeds are economical for aquaculture for a maximal production/cost ratio. An integrated intensive aquaculture approach, such as fish or shrimp culture associated with shellfish and/or seaweeds, is currently under development and shows economical and environmental sustainability (Neori et al. 2004).

The herbivorous fish tool will be further enhanced and developed, in particular to better identify herbivorous fish–seaweed species pairings for aquaculture usage. However, food items and diet information for many herbivorous fishes are quite lacking in the literature. These research gaps must be filled in the coming years by further studies on species that lack any record. The herbivorous tool provides a list of these species. Moreover, detritivory might be more important than herbivory in some fishes known to be herbivores, which could impact aquaculture practices such as facilitating sedimentation to create EAM.

Acknowledgements The authors profoundly thank Dr. Masao Ohno, who supported the senior author to attend the 19th International Seaweed Symposium and Lotta Jarnmark, Incofish Project WP1 for support. We acknowledge the FishBase team for the data encoded and assistance provided on web programming of the herbivorous fish tool, and an anonymous reviewer for comments and suggestions. This is WorldFish Center Contribution No. 1846.

References

Andrew NL, Jones GP (1990) Patch formation by herbivorous fish in a temperate Australian kelp forest. Oecologia 85:57–68

Benavides AG, Cancino JM, Ojeda FP (1994) Ontogenetic change in the diet of *Aplodactylus punctatus* (Pisces: Aplodactylidae): an ecophysiological explanation. Mar Biol 118:1–5

Cetrulo GL, Hay ME (2000) Activated chemical defenses in tropical versus temperate seaweeds. Mar Ecol Prog Ser 207: 243–253

Choat JH, Clements KD, Robbins WD (2002) The trophic status of herbivorous fishes on coral reefs. I. Diet analyses. Mar Biol 140:613–623

Clements KD, Choat JH (1993) Influence of season, ontogeny and tide on the diet of the temperate marine herbivorous fish *Odax pullus* (Odacidae). Mar Biol 117:213–220

Cronin G, Hay ME (1996) Within-plant variation in seaweed palatability and chemical defenses: optimal defense theory versus the growth-differentiation balance hypothesis. Oecologia 105:361–368

Cronin G, Valerie JP, Hay ME, Fenical W (1997) Are tropical herbivores more resistant than temperate herbivores to seaweed chemical defenses? diterpenoid metabolites from *Dictyota acutiloba* as feeding deterrents for tropical versus temperate fishes and urchins. J Chem Ecol 23:289–302

Crossman DJ, Choat JH, Clements KD, Hardy T, McConochie J (2001) Detritus as food for grazing fishes on coral reefs. Limnol Oceanogr 47:1596–1605

Crossman DJ, Choat JH, Clements KD (2005) Nutritional ecology of nominally herbivorous fishes on coral reefs. Mar Ecol Prog Ser 296:129–142

Duffy JE, Paul VJ (1992) Prey nutritional quality and the effectiveness of chemical defenses against tropical reef fishes. Oecologia 90:333–339

Edwards TW, Horn MH (1982) Assimilation efficiency of a temperate-zone intertidal fish (*Cebidichthys violaceus*) fed diets of macroalgae. Mar Biol 67:247–253

Erickson AA, Paul VJ, Van Alstyne KL, Kwiatkowski LM (2006) Palatability of macroalgae that use different types of chemical defenses. J Chem Ecol 32:1883–1895

Floeter SR, Behrens MD, Ferreira CEL, Paddack MJ, Horn MH (2005) Geographical gradients of marine herbivorous fishes: patterns and processes. Mar Biol 147:1435–1447

Froese R, Pauly D (eds) (2007) FishBase. World wide web electronic publication. http://www.fishbase.org. Cited February 2007

Guiry MD, Guiry GM (2007) AlgaeBase version 4.2. World-wide electronic publication, National University of Ireland, Galway. http://www.algaebase.org. Cited 14 March 2007

Hay ME (1984) Predictable spatial escapes from herbivory: how do these affect the evolution of herbivore resistance in tropical marine communities? Oecologia 64:396–407

Hay ME (1997) The ecology and evolution of seaweed-herbivore interactions on coral reefs. Coral Reefs 16:68–76

Horn M (1989) Biology of marine herbivorous fishes. Oceanogr Mar Biol Annu Rev 27:167–272

Horn MH, Messer KS (1992) Fish guts as chemical reactors: a model of the alimentary canals of marine herbivorous fishes. Mar Biol 113:527–535

Horn MH, Murray SN, Edwards TW (1982) Dietary selectivity in the field and food preferences in the laboratory for two herbivorous fishes (*Cebidichthys violaceus* and *Xiphister mucosus*) from a temperate intertidal zone. Mar Biol 67:237–246

Horn MH, Neighbors MA, Murray SN (1986) Herbivore response to a seasonally fluctuating food supply: growth potential of two temperate intertidal fishes based on the protein and energy assimilated from their macroalgal diets. J Exp Mar Biol Ecol 103:217–234

Jones GP, Andrew NL (1990) Herbivory and patch dynamics on rocky reefs in temperate Australasia: the roles of fish and sea urchins. Aust J Ecol 15:505–520

Keshavanath P, Gangadhar B, Ramesh TJ, van Dam AA, Beveridge MCM, Verdegem MCJ (2002) The effect of periphyton and supplemental feeding on the production of the indigenous carps *Tor khudree* and *Labeo fimbriatus*. Aquaculture 213:207–218

Lewis SM (1985) Herbivory on coral reefs: algal susceptibility to herbivorous fishes. Oecologia 65:370–375

Montgomery WL, Gerking SD (1980) Marine macroalgae as foods for fishes: an evaluation of potential food quality. Env Biol Fish 5:143–153

Muñoz AA, Ojeda FP (2000) Ontogenetic changes in the diet of the herbivorous *Scartichthys viridis* in a rocky intertidal zone in central Chile. J Fish Biol 56:986–998

Neighbors MA, Horn MH (1991) Nutritional quality of macrophytes eaten and not eaten by two temperate-zone herbivorous fishes: a multivariate comparison. Mar Biol 108:471–476

Neori A, Chopin T, Troell M, Buschmann AH, Kraemer GP, Halling C, Shpigel M, Yarish C (2004) Integrated aquaculture: rationale, evolution and state of the art emphasizing seaweed biofiltration in modern mariculture. Aquaculture 231:361–391

Ochavillo DG, Dixon PI, Aliño PM (1992) The daily food ration of parrotfishes in the fringing reefs of Bolinao, Pangasinan, Northwestern Philippines. Proceedings 7th International Coral Reef Symposium. Guam 2:927–933

Ojeda FP, Muñoz AA (1999) Feeding selectivity of the herbivorous fish *Scartichthys viridis*: effects on macroalgal community structure in a temperate rocky intertidal coastal zone. Mar Ecol Prog Ser 184:219–229

Paul VJ, Hay ME (1986) Seaweed susceptibility to herbivory: chemical and morphological correlates. Mar Ecol Prog Ser 33:255–264

Pauly D, Sa-a P (2000). Estimating trophic levels from individual food items. In: Froese R, Pauly D (eds) FishBase 2000: concepts, design and data sources. ICLARM, Los Baños, Laguna, Philippines, p 185

Pillans RD, Franklin CE, Tibbetts IR (2004) Food choice in *Siganus fuscescens*: influence of macrophyte nutrient content and availability. J Fish Biol 64:297–309

Sa-a P, Palomares ML, Pauly D (2000) The FOOD ITEMS table. In: Froese R, Pauly D (eds) FishBase 2000: concepts, design and data sources. ICLARM, Los Baños, Laguna, Philippines, pp 182–188

Steinberg PD (1986) Chemical defenses and the susceptibility of tropical marine brown algae to herbivores. Oecologia 69:628–630

Wilson SK, Bellwood DR, Choat JH, Furnas MJ (2003) Detritus in the epilithic algal matrix and its use by coral reef fishes. Oceanogr Mar Biol Annu Rev 41:279–309