Interactions of pelagic cnidarians and ctenophores with fish: a review

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Abstract

Medusae, siphonophores and ctenophores (here grouped as 'pelagic coelenterates') interact with fish in several ways. Some interactions are detrimental to fish populations, such as predation by gelatinous species on pelagic eggs and larvae of fish, the potential competition for prey among pelagic coelenterates and fish larvae and zooplankt-ivorous fish species, and pelagic coelenterates serving as intermediate hosts for fish parasites. Other interactions are positive for fish, such as predation by fish on gelatinous species and commensal associations among fish and pelagic coelenterates. The interactions range from beneficial for the gelatinous species (food, parasite removal), to negative (predation on them). We review existing information and present new data on these topics. Although such interactions have been documented frequently, the significance to either fish or pelagic coelenterate populations is poorly understood. The effects of pelagic coelenterates on fish populations are of particular interest because of the great importance of fisheries to the global economy. As fishing pressures mount, it becomes increasingly important to understand how they may influence the balance between pelagic coelenterates and fish.

Introduction

The relationships between pelagic coelenterates and fish have been of particular interest because of the potential effects on commercially important fisheries. Although pelagic coelenterates generally are known for being deleterious to fish and fisheries (e.g. Hay et al., 1990), the interactions potentially are both negative and positive. Such interactions include predation on ichthyoplankton by pelagic coelenterates (reviewed in Möller, 1980; Purcell, 1985, 1997; Arai, 1988; Bailey & Houde, 1989), potential competition between pelagic coelenterates and zooplanktivorous fish and fish larvae for prey (op. cit.), predation by fish on medusae and ctenophores (reviewed by Arai, 1988; Ates, 1988; Harbison, 1993), parasite transmission to fish (Lauchner, 1980a,b; Arai, 1988), and commensal

associations between fish and medusae (reviewed in Mansueti, 1963; Thiel, 1970, 1978).

Unfortunately, we know little about the significance of most of the above interactions for either fish or pelagic coelenterate populations. The most data exist for pelagic coelenterates as predators on ichthyoplankton. Descriptive information for the other types of interactions usually is without any understanding of the potential importance. Herein, we review existing information on the various interactions among fish and pelagic coelenterates, a term we use to include scyphomedusae, hydromedusae, cubomedusae, siphonophores and ctenophores. We discuss these interactions and the possibility of increasing pelagic coelenterate populations in the context of global changes that are occurring due to commercial fishing activities (Parsons, 1995; Pauly et al., 1998a).

Predation by pelagic coelenterates on fish eggs and larvae

Predator types and characteristics

Gelatinous predators of ichthyoplankton range from a few, highly specific predators, like cystonect siphonophores, to many species with broad diets (Purcell, 1997). Species that include high proportions of soft-bodied prey in their diets often eat many fish eggs and larvae when available (Purcell, 1997). The cystonect siphonophores eat mainly larval fish (94–100% of the diets), and other soft-bodied organisms (chaetognaths, small squids) are also eaten by *Physalia physalis* (Linnaeus) (see Purcell, 1984b). The diet of the hydromedusan *Aequorea victoria* (Murback & Shearer) consists almost exclusively of Pacific herring (*Clupea pallasi* Valenciennes) larvae when the larvae first hatch (Purcell, 1989; Purcell & Grover, 1990), and includes a variety of larvae of other fish families (Pleuronectidae, Cottidae, Scorpaenidae, Stichaeidae, Pholidae and Gadidae), as well as pelagic eggs from pleuronectids, in addition to gelatinous and crustacean prey (Purcell, 1989). Diets of semaeostome scyphomedusae, such as *Aurelia aurita* (Linnaeus), *Cyanea capillata* (Linnaeus) and *Chrysaora quinquecirrha* (Desor), may also contain large numbers of ichthyoplankton prey in addition to gelatinous and crustacean prey (Möller, 1980, 1984; Fancett, 1988; Purcell et al., 1994b). For example, gut contents of *C. quinquecirrha* may contain as many as 1497 eggs and 71 larvae medusa^{-1}.

Gelatinous predators that consume primarily crustacean prey usually contain few fish eggs or larvae at typical ichthyoplankton densities (reviewed in Purcell, 1997). For example, hydromedusae like *Sarsia tubulosa* (M. Sars), which eat mostly crustaceans (Purcell, 1990), contained few fish larvae (0 in 2 100 medusae) at low larval densities (<0.5 m^{-3}; Van Der Veer, 1985), but contained several Pacific herring larvae (17 in 38 medusae) at high larval densities (mean 632 m^{-3}; Purcell, 1990). Some species of cubomedusae frequently eat post-larval fish, while other species eat mainly prawns or copepods, however, the information available is mostly qualitative (Larson, 1976; Hamner et al., 1995; Stewart, 1996). For example, *Carukia barnesi* Southcott eats almost exclusively fish and *Chironex fleckeri* Southcott eats prawns when small, but switches to fish when about 80 mm in bell diameter (J. Seymour, pers. comm.).

Likewise, the incidence of fish larvae in the gut contents of ctenophores is generally low, however, predation on fish eggs by lobate ctenophores can be substantial. Among cydippid species, only 0.06% of 15 000 *Pleurobrachia pileus* (O. F. Müller) contained fish larvae (Van Der Veer, 1985), about 5% of 710 *P. bachei* L. Agassiz contained herring larvae at high densities near hatching (Purcell, 1990). None of 75 lobate *Mnemiopsis leidyi* A. Agassiz from Chesapeake Bay contained bay anchovy larvae, while one-third contained 1–3 eggs (Purcell et al., 1994b). Ichthyoplankton also compose a small proportion of the prey items of ctenophores in the Black Sea. Ichthyoplankton averaged 1% of the prey items of *P. pileus* averaged over six cruises, but the highest percentage (10%) was on one cruise in July, 1992 (Mutlu & Bingle, 1999). Similarly, fish eggs or larvae averaged 0.12% of the prey items in *M. leidyi*, but reached 4% during one (August, 1993) of the six cruises (Mutlu, 1999). Nevertheless, because of their great abundance during the spawning season of pelagic schooling fish, *M. leidyi* can consume substantial proportions of those ichthyoplankton (reviewed by Purcell et al., 2001).

Selection for fish eggs and larvae by gelatinous predators has been positive for every species for which it has been calculated: scyphomedusae *Cyanea capillata*, *Pseudorhiza haeckeli* Haacke, *Stomolophus meleagris* L. Agassiz, *Chrysaora quinquecirrha* (in Fancett, 1988; Larson, 1991; Purcell et al., 1994b); hydromedusae *Aequorea victoria* (in Purcell, 1989); and cystonect siphonophores (Purcell, 1981b, 1984b). Fish eggs and yolk-sac larvae may be positively selected by the medusae because they have little or no escape ability, and they are large relative to most other zooplankton, thereby increasing encounter rates.

Factors affecting pelagic coelenterate encounter and capture of ichthyoplankton

Feeding rates of gelatinous species on ichthyoplankton depend on several factors that affect encounter rates between the predator and prey, and subsequent capture. This has been reviewed in Purcell (1985), Arai (1988), Arai (1997) and Purcell (1997), therefore we will discuss the factors briefly as they apply to ichthyoplankton. Thickness and spacing of the tentacles affect encounters of tentaculate predators with prey (Madin, 1988; Purcell, 1997). This is reflected by the general trend of predators having numerous, closely-spaced tentacles eating smaller prey than predators

with few, widely-spaced tentacles (op. cit.). This trend holds in general terms, with the first group eating mostly crustacean prey, and the second group including soft-bodied prey, like fish larvae, in the diets.

Some taxa swim while feeding ('cruising', e.g., scyphomedusae, some hydromedusae, lobate ctenophores), and others do not swim while feeding ('ambush', e.g. siphonophores, some hydromedusae, cydippid ctenophores). Cruising predators are predicted to capture predominantly small, slow prey, while ambush predators are predicted to capture mostly larger, faster prey (Gerritsen & Strickler, 1977; Greene, 1986). Those trends hold to a degree among the predators of ichthyoplankton. For example, fish eggs do not swim and are eaten in great numbers by cruising taxa like scyphomedusae, *Aequorea victoria*, and *Mnemiopsis leidyi* (Table 1), but are not eaten much by ambush taxa like siphonophores or *Pleurobrachia bachei* (Purcell, 1981a, 1990; Van Der Veer, 1985). Post-yolksac fish larvae are active swimmers, and are eaten in large numbers by some ambush taxa (cystonect siphonophores), and are not eaten much by some cruising predators (*M. leidyi)*. There are obvious exceptions to these trends as well, for example, the cruising scyphomedusae and *A. victoria* capture many fish larvae.

Trends in prey capture by cnidarians are related to the types of nematocysts present, with soft-bodied prey, including fish larvae, being captured by predators such as cystonect siphonophores that have only a few types of nematocysts, which penetrate prey, and hard-bodied prey being captured by predators such as most siphonophores and hydromedusae that have several types of nematocysts, some of which adhere to prey (Purcell, 1984a; Purcell & Mills, 1988). Most of the various predators, such as scyphomedusae, have a mix of nematocysts types, and include both hard and soft-bodied prey in the diets (Purcell, 1997). Chemical stimuli from the prey may also affect nematocyst discharge and the types of prey captured (Purcell & Anderson, 1995).

Characteristics of the prey, such as size, stage and swimming speed, also affect their encounter rates with the predators and abilities to escape (reviewed by Purcell, 1985; Bailey & Houde, 1989). Fish eggs do not swim, small yolk-sac larvae swim weakly and larger post-yolksac larvae swim with increasing speed as they grow (Bailey, 1984; Purcell et al., 1987). Increased size and swimming speed would increase encounter rates with predators, but also increase escapes from the predators. For example, yolksac herring larvae escaped in only 9% of contacts with *Aequorea victoria* tentacles, while post-yolksac larvae escaped from 87% of contacts (Purcell et al., 1987). Most studies show greater feeding on yolksac larvae than on post-yolksac larvae (Bailey, 1984; Purcell et al., 1987), and on small larvae than on large (Cowan & Houde, 1992, 1993), however, the opposite trend was observed for the large hydromedusa *Staurophora mertensi* Brandt feeding on capelin (*Mallotus villosus*) larvae (De Lafontaine & Leggett, 1988). Also, unfed larvae show reduced swimming compared with fed larvae, which reduces encounters and escapes (Bailey, 1984). This is reflected in greater capture of unfed larvae than fed (Bailey, 1984; Purcell et al., 1987).

Several studies incorporate characteristics of both gelatinous predators and ichthyoplankton prey in individual-based models in order to predict encounter and predation rates (Bailey & Batty, 1983; Cowan & Houde, 1992; Cowan et al., 1996; Paradis et al., 1996, 1999; Breitburg et al., 1999). All of these models have been based on the encounter theory of Gerritsen & Strickler (1977). They use experimental measurements of swimming speeds, encounter radius (size), and densities of both predator and prey organisms, and predation rates to determine encounter probabilities. Most of the studies focus on the effects of size on predation. Encounter and predation rates increase with diameter for *Aurelia aurita* medusae (5–21 mm) (Bailey & Batty, 1984). Susceptibility (the probability of capture after contact) of bay anchovy decreases rapidly with larval size (3–9 mm) to both *Mnemiopsis leidyi* ctenophores and *Chrysaora quinquecirrha* medusae, but the percent eaten is relatively constant with larval size (Cowan & Houde, 1992). Predation rate *versus* prey:predator length is maximum when prey size is about 10% of predator size, decreasing linearly at greater percentages from combined data on 5 species of medusae from 9 studies; a dome-shaped relationship resulted for *M. leidyi* ctenophores combined from 3 studies (Paradis et al., 1996). Other studies extend the models to predict survival and growth of ichthyoplankton *in situ* (Cowan et al., 1997; Breitburg et al., 1999).

Predation rates and effects on ichthyoplankton populations

Feeding rates of gelatinous species on ichthyoplankton show some important general trends. We use 'feeding rates' to include both 'clearance rates' (liters cleared predator^{-1} d^{-1}) and 'predation rates' (numbers of

Table 1. Predation rates, clearance rates and predation effects of gelatinous predators feeding on fish eggs and larvae. Medusa sizes are bell diameters, and ctenophore sizes are in ml live volume. Prey consumed are the estimated percentages consumed daily *in situ*.

Predator species and size	Condition	Prey type and density (No. prey m^{-3})	Prey eaten (No. pred^{-1} d^{-1})	Clearance rates[h] (l pred^{-1} d^{-1})	Prey consumed (% d^{-1})	Source
Physalia physalis	Field	~0.2 larvae m^{-3a}	120	600 000	60.0	Purcell (1984b)
Rhizophysa eysenhardti	Field	28 larvae m^{-3a}	9	311	28.3	Purcell (1981b)
Aequorea victoria 33–68 mm	Field	< 10 larvae m^{-3b}	13±13	5650±6114	18±29	Purcell (1989, 1990); Purcell & Grover (1990)
		10–100 larvae m^{-3b}	55±48	1357±908	49±35	
		>100 larvae m^{-3b}	91±47	288±210	33±32	
Nemopsis bachei 0.6 ml	2.2 m^3	23–90 eggs m^{-3c}	4±3	72.9^i, 40.5	na	Cowan et al. (1992)
Aurelia aurita 6–50 mm	Field	larvae^d	1.6	na	2.6–4.4	Möller (1980)
35–50 mm	0.27 m^3	larvae 96–3704 m^{-3e}	na	204±69	na	De Lafontaine & Leggett (1987)
40–80 mm	6.3 m^3	larvae 39–410 m^{-3e}	na	526±173	na	De Lafontaine & Leggett (1987)
40–85	5 m^3	10–80 larvae m^{-3d}	na	182	na	Gamble & Hay (1989)
na	2 m^3	50 larvae m^{-3f}	na	na	1.0–5.8^{g,h}	Duffy et al. (1997)
Chrysaora quinquecirrha 53 ml^h, 39 ml	Lab, 750l	33–133 eggs m^{-3g}	110±67	1383^i, 885	20–40	Cowan & Houde (1993)
100 mm–calc av	3.0 m^3	20 eggs m^{-3g}	68±28^i	2983±788^i	20–40	Cowan & Houde (1993)
40–70 mm	Field	av. 164 eggs m^{-3g}	343±419	2213±1625	14±4	Purcell et al. (1994b)
na	2.0 m^3	50 larvae m^{-3f}	na	na	0.1–10.4^{g,h}	Duffy et al. (1997)
36 ml^h, 52.5 ml	3.0 m^3	10 larvae m^{-3g}	6^i,13	1344^i, 630	20–40	Cowan & Houde (1993)
40–70 mm	Field	av. 43 larvae m^{-3g}	86±136	1818±1861	29±14	Purcell et al. (1994b)
Cyanea capillata 40 mm	Lab, 25 l	eggs and larvae^a	na	140 ^{i}	0.1-2.4	Fancett & Jenkins (1988)
Pseudorhiza haeckeli 40 mm	Lab, 25 l	eggs and larvae^a	na	400^i	0.1–3.8	Fancett & Jenkins (1988)
Stomolophus meleagris 55 mm	Field	eggs^a	na	3120	na	Larson (1991)
na	2.0 m^3	50 larvae m^{-3f}	na	na	0.3–15.8^{g,h}	Duffy et al. (1997)
Mnemiopsis leidyi 13 ml	Lab, 200 l	eggs^g	na	60–170	10–65	Monteleone & Duguay (1998)
15–16 ml	LAb, 750 l	33–133 eggs m^{-3g}	10^i, 7	128^i, 82	20–40	Monteleone & Duguay (1988)
3 ml	2.2 m^3	45 eggs m^{-3g}	2–5	50±46	38	Cowan et al. (1992)
17 ml	3.0 m^3	20 eggs m^{-3g}	7±1^i	366±58^i	20–40	Cowan & Houde (1993)
40 ml	Field	224±178 eggs m^{-3g}	42±33	128±58	9±14	Purcell et al. (1994b)
21 ml	3.0 m^3	10 larvae m^{-3g}	1.7^i, 0.1	172^i, 15	20–40	Cowan & Houde (1992, 1993)
40 ml	Field	av. 43 larvae m^{-3g}	0	0	0	Purcell et al. (1994b)

[a]Mixed species or unidentified; [b]Pacific herring, [c]Black drum, *Pogonias cromis* (Linnaeus); [d]Atlantic herring, *Clupea harengus* Linnaeus; [e]Capelin, *Mallotus villosus* (Müller); [f]Red drum, *Sciaenops ocellatus* Linnaeus, ranges represent 1-2 d old to 12-13 d old larvae; [g]Bay anchovy; [h]calculated from data in source; [i]with no alternative prey; na = not available. Data on *Mnemiopsis leidyi* in the Black Sea are not included here, but are summarized in Purcell et al. (2001).
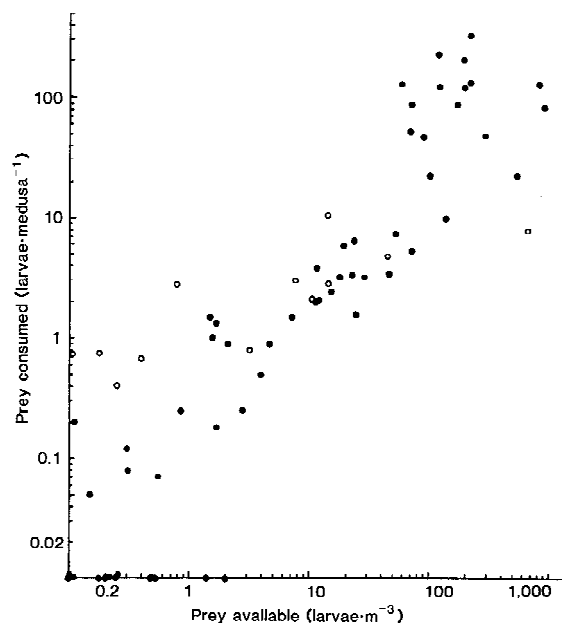
Figure 1. Predation rates by the hydromedusan *Aequorea victoria* relative to density of Pacific herring larvae in two locations on Vancouver Island, British Columbia, Canada. Data are compiled from 1983 to 1987. Each point represents averages for several medusae at individual stations. Daytime (○); nighttime (●). Data sources as in Table 2.

prey eaten predator^{-1} d^{-1}), and distinguish between the two when appropriate. Increasing size of the predator increases the predation rates (Table 1). For example, small species like *Nemopsis bachei* L. Agassiz (0.6 ml volume) consumed only 4 eggs medusa^{-1} d^{-1}, while large species like *Chrysaora quinquecirrha* (≤100 ml) ate 100 or more eggs daily (Table 1). Within a species, feeding rates on ichthyoplankton increase with medusa size, as shown for *Aurelia aurita* (Möller, 1980; Bailey & Batty, 1984; Gamble & Hay, 1989) *Cyanea capillata* (Fancett & Jenkins, 1988), and *C. quinquecirrha* (Purcell et al., 1994b).

In addition to the sizes of pelagic coelenterates and prey, predation rates (prey eaten predator^{-1} d^{-1}) of eggs and larvae increase directly with prey density (Bailey & Batty, 1984; De Lafontaine & Leggett, 1987; Fancett & Jenkins, 1988; Purcell et al., 1994b). Large gelatinous species feeding at high densities of ichthyoplankton may eat tens to hundreds of fish eggs and larvae daily (Table 1). For example, predation by the large hydromedusan, *Aequorea victoria*, increased over four orders of magnitude and larval herring densities similarly differed over four orders of magnitude (Fig. 1). Low prey densities, which are

common in ocean waters, can make accurate estimates of predation on ichthyoplankton difficult *in situ*.

Experimental conditions greatly affect the feeding rates obtained. Experiments in small containers sometimes appear to overestimate predation, perhaps because the prey become trapped by the predators, and because extremely high prey densities often are used. Predation rates are negatively correlated with container size and experiment duration for medusae and ctenophores (Paradis et al., 1996). Counter to those results, small containers appear to disturb feeding by pelagic coelenterates, and predation rates sometimes increase with container size (Table 1; De Lafontaine & Leggett, 1987; Toonen & Chia, 1993). Nevertheless, those opposing trends lead to the same conclusion, that experiments in small containers do not yield realistic results. Additionally, consumption of ichthyoplankton is much greater in experiments without alternative prey than when zooplankton also is present (Table 1, Cowan & Houde, 1992, 1993). The effects of predator and prey species, sizes, prey density, container size and the presence of alternative prey, which differ among the various studies, make comparisons difficult.

It is possible to compare among predator species and prey types by using clearance rates, indicating the 'volume swept clear', which generally do not vary with prey density at natural levels (Purcell, 1997). Satiation at high larval densities may occur in laboratory experiments and in the field, however, as suggested by the decrease in clearance rates of *Aequorea victoria* with increasing density of large Pacific herring larvae *in situ* (Table 1). Field estimates show that large medusae can clear > 1 m^3 of ichthyoplankton daily (Table 1). Individual clearance rates of bay anchovy, *Anchoa mitchilli* (Valenciennes), eggs and larvae for the lobate ctenophore, *Mnemiopsis leidyi*, are about an order of magnitude lower than for the scyphomedusan, *Chrysaora quinquecirrha* in Chesapeake Bay (Table 1). Clearance rates standardized to predator volume are more similar, but still greater for the medusae (21.2±2.8 versus 39.0±6.7 l ml predator^{-1} d^{-1}) (Cowan & Houde, 1993). Clearance rates differ dramatically with prey type for any given predator, for example, *C. quinquecirrha* clears only 16 l medusa^{-1} d^{-1} of copepods (Purcell, 1992), but clears hundreds to thousands of liters daily of ichthyoplankton (Table 1). Clearance rates (Table 1) on fish larvae are lower than for fish eggs, which have large diameters and no escape abilities.

Table 2. Consumption of newly-hatched herring larvae by the hydromedusan *Aequorea victoria* on Vancouver Island, British Columbia, Canada. Data are averages of 3 stations in both locations

Location and date	No. of medusae examined	Larvae in each medusa (No.)	Medusae m^{-3}	Larvae m^{-3}	% larvae eaten d^{-1}
Kulleet Bay					
22 Mar 1983[a]	24	22.0	0.012	162.1±284.6	0.8
9 Apr 1984[b]	12	2.0	0.35	38.5	11.1
14–21 Apr 1985[c]	322	0.2–135.3	1.1–5.1	3.5–264.1	40.5–72.8
31 Mar 1986[d]	10	3.1	<0.006	19.3	0.7
31 Mar–2 Apr 1987[d]	33	51.3	0.02	145.6±263.6	4.6
Baynes Sound					
20–21 Mar 1983[d]	201	0.04–2.4	0.01–0.43	0.8–29.0	2.5–8.9
6–7 Apr 1984[d]	79	0.06–0.4	0.1–0.4	43.1–62.5	0.4
30 Mar 1985[d]	12	0.08	0.5±0.4	3.4±3.7	7.7
30 Mar 1986[d]	9	3.1	0.03	29.8±14.0	2.1
30 Mar 1987[d]	13	3.2	<0.0002	47.6±30.0	<0.1

[a]Purcell (1989); [b]from Purcell (1990); [c]from Purcell & Grover (1990); [d]Purcell (unpublished data).

Predation effects by pelagic cnidarians on fish larvae often are substantial (>30% d^{-1}) in environments where predators are numerous, as for the scyphomedusan *Chrysaora quinquecirrha*, the hydromedusan *Aequorea victoria*, and the siphonophores *Rhizophysa eysenhardti* Gegenbaur and *Physalia physalis* (Purcell, 1981b, 1984b, 1992; Purcell & Grover, 1990). The magnitude of predation depends critically on predator population size, as illustrated for *A. victoria* at two locations in British Columbia, Canada, where medusa densities differed over four orders of magnitude and predation differed from < 0.1 to 73% d^{-1} (Table 2). By contrast, effects of ctenophores on fish larvae are small (e.g. Van Der Veer, 1985; Purcell et al., 1994b, 2001), but lobate ctenophores may have large effects on fish eggs (10–65% d^{-1}, Monteleone & Duguay, 1988; 0–40% d^{-1}, Cowan & Houde, 1993; Purcell et al., 1994b, 2001). Intense daily predation on ichthyoplankton can have serious consequences because the spawning period of the fish may be limited (e.g. Pacific herring spawn once annually). Inverse correlations in predator and larval fish abundances have been interpreted as predation effects (e.g. Alvariño, 1980; Möller, 1984), however, there can be other explanations for such negative relationships (Frank & Leggett, 1985; Purcell, 1985). Unless supported by more direct evidence, inverse correlations should not be used as indicators of predation effects.

Competition for food among pelagic coelenterates and fish

The diets of many species of gelatinous predators include mostly copepods, cladocerans, larvaceans and meroplanktonic invertebrate larvae in different proportions depending on predator species and prey availability (summaries in Purcell, 1981a; Purcell & Mills, 1988; Mills, 1995; Arai, 1997; Purcell, 1997), and overlap with the diets of zooplanktivorous fish, such as anchovies, herrings and sardines. Although several authors have speculated on the importance of potential competition among zooplanktivorous pelagic coelenterates and fish (e.g. Möller, 1980; Van Der Veer, 1985; Arai, 1988, 1997; Bailey & Houde, 1989; Shiganova, 1998), very few direct comparisons of diets have been made. Purcell & Grover (1990) compare the diets of post-yolksac larval Pacific herring and those of seven co-occurring hydromedusan species. The prey of larval herring (copepod nauplii and eggs, shelled protozoans and bivalve veligers) were abundant (41 l^{-1}) in the environment, and predation on those prey by the gelatinous species was estimated to be only 0.2% d^{-1} of the standing stocks. They conclude that competition for food among the larvae and pelagic coelenterates was not occurring at that time. Consumption of mesozooplankon by the introduced ctenophore *Mnemiopsis leidyi* and zooplanktivorous fish (European anchovy, *Engraulis encrasicolus* (Lin-

Table 3. Percent diet similarities (Schoener, 1974) among species of jellyfish and forage fish in PWS. The similarities among mainly crustacean-eating species (top left) and among mainly larvacean-eating species (bottom right) are highlighted (Purcell & Sturdevant, 2001)

	Percent Diet Similarity (%)			
	Walleye pollock	Pacific sandlance	Pacific herring	Pink salmon
Aurelia labiata	67.2	75.1	73.3	18.7
Pleurobrachia bachei	41.1	63.4	62	5.3
Cyanea capillata	34.8	33.7	50.2	78.1
Aequorea aequorea	55.5	35.5	48.9	59.0

naeus), European sprat, *Sprattus sprattus* (Linnaeus) and Mediterranean horse mackerel, *Trachurus mediterraneus* (Steindachner)) in the Black Sea are estimated by Vinogradov et al. (1996). Biomass of zooplankton and fish, and prey consumption by fish were high until 1988, but decreased dramatically during the outbreak period of *M. leidyi* that began in 1989. Competition for food among the ctenophores and fish was inferred.

Purcell & Sturdevant (2001) quantify the diets of four gelatinous species and the zooplanktivorous juveniles of four fish species in Prince William Sound, Alaska. *Aurelia labiata* Chamisso & Eysenhardt and *Pleurobrachia bachei* eat mostly hard-bodied prey, such as small copepods, cladocerans and bivalve veligers, and *Cyanea capillata* and *Aequorea aequorea* var. *albida* Bigelow consume mostly larvaceans, with some crustacean prey. The juvenile fish all consume some of each zooplankton taxon, however, walleye pollock, *Theragra chalcogramma* (Pallas), Pacific sandlance, *Ammodytes hexapterus* Pallus, and Pacific herring eat mainly small copepods, but pink salmon, *Oncorhynchus gorbuscha* (Walbaum) consumed mostly larvaceans. Percent Similarity Index (PSI) values comparing the diets of the gelatinous and juvenile fish show the greatest similarities among crustacean-eating species (*A. labiata*, 67–75%; *P. bachei*, 41–62%) with walleye pollock, Pacific sandlance and Pacific herring), and among larvacean-eating species (*C. capillata*, 78%; *A. aequorea*, 59%) with pink salmon (Table 3). PSI comparisons among all pelagic coelenterate and fish species average 50%.

The potential for competition for zooplankton prey among fish and pelagic coelenterates is very difficult to assess. Determination of all the necessary parameters has not been encompassed by any study, to

our knowledge. Whether competition would occur depends on the extent of the spatial, depth and temporal co-occurrence of the various species, as well as their consumption rates of zooplankton, and the production rates of the zooplankton. In addition, demonstrating competition would require evidence that prey populations are limited by predation.

Generally, estimated predation effects of gelatinous species on copepod populations are too small to cause prey population declines (e.g. $<10\%$ d^{-1}; Kremer, 1979; Larson, 1987a; Kuipers et al., 1990; Purcell et al., 1994a). Other studies, however, indicate much higher predation and possible reduction of zooplankton standing stocks (e.g. $>20\%$ d^{-1}; Deason, 1982; Matsakis & Conover, 1991; Purcell, 1992; Olesen et al., 1994; Schneider & Behrends, 1998; Purcell et al., 2001). Inverse relationships in the abundances of gelatinous predators and zooplankton often have been interpreted as resulting from predation (e.g. Feigenbaum & Kelly, 1984; Behrends & Schneider, 1995). Correlations do not show cause and effect and may be misleading, as for mid-Chesapeake Bay, where gelatinous predators were not responsible for the spring decline of copepods in 1987 and 1988 (Purcell et al., 1994a).

Associations among pelagic coelenterates and fish

Associations of fish species with pelagic coelenterates include no cases that are species-specific and obligate partnerships. Even in the classic example of the man-of-war fish, *Nomeus gronovii* (Gmelin), with the pleustonic siphonophore, *Physalia physalis*, the fish occur with alternative hosts, and the siphonophore with six other fish species. *N. gronovii* remains as an adult in the association, and survives with this extremely toxic host due to a variety of special characteristics (reviewed in Arai, 1988). The fish has at least one antibody to the toxins and can survive high doses, but is not completely immune. It has a complex skin structure that may reduce nematocyst penetration. The fish is very flexible due to an unusually large number of vertebrae, and actively avoids contact with the tentacles. In this association, the fish is known to feed on the siphonophore, as well as be eaten (Jenkins, 1983).

Observations of fish associated with siphonophores other than *Physalia physalis* are rare. Biggs (1976) reports juvenile fish with camouflaging pigmentation sheltered among the tentacles of *Forskalia*

tholoides Haeckel, and Robison (1983) reports California smoothtongue, *Leuroglossus stilbius* Gilbert, and a myctophid, *Stenobrachius leucopsarus* (Eigenmann & Eigenmann), associated with midwater siphonophores, *Apolemia* sp.

Few observations of fish associated with ctenophores exist. Several fish species, *Chloroscombrus chrysurus* (Linnaeus), *Hemicaranx amblyrhynchus* (Cuvier), *Palinurichthys* sp., *Syngnathus* sp. and P*eprilus alepidotus* (Linnaeus), are reported with *Beroe* sp. in the Gulf of Mexico (Matthews & Shoemaker, 1952), where larval spadefish, *Chaetodipterus faber* (Broussonet), are seen laying between the comb rows of *Beroe* sp. (A. G. Moss, pers. comm.). Several unidentified myctophid fish have been observed among groups of unidentified ctenophores (Auster et al., 1992).

The most common associations are among juvenile fish and scyphomedusae (reviewed in Mansueti, 1963; Thiel, 1970, 1978; Arai, 1997; Table 4). Although at least 80 species pairs have been documented (op. cit.), those represent a small fraction of the possible combinations of species. These non-specific, facultative associations occur mainly between scyphomedusae and juvenile fish in the families Carangidae, Stromateidae and Gadidae, although some associations with species in at least six additional families are recorded. Several fish species within a genus may associate with pelagic coelenterates. Typically, a given fish species may be found consorting with more than one gelatinous species. For example, ROV observations show up to five age-0 walleye pollock swimming among tentacles of *Cyanea capillata* and up to 30 with *Chrysaora melanaster* Brandt at depths of 30–40 m during the day in Alaskan waters (Brodeur, 1998). Juveniles of several fish species may associate with a species of medusa, either under the swimming bell or near the tentacles of semaeostomes, and often schooling in front of the bell of rhizostomes. The fish seek refuge among the tentacles and oral arms or in the sub-genital pouches when frightened. Several fish typically consort with an individual medusa, however, schools of juvenile walleye pollock were associated with aggregations of *Aurelia labiata* medusae in Alaska (Purcell et al., 2000).

It generally is assumed that through associations with pelagic coelenterates, the fish gain protection from vertebrate predators. Only post-larval fish are seen consorting with pelagic coelenterates, however, presumably because larvae would be eaten. Protection from predators has been demonstrated in only one study, in which juvenile American butterfish, *Peprilus triacanthus* (Peck), were eaten by birds when displaced from their scyphomedusan host, *Cyanea capillata* (in Duffy, 1988). The potential benefits of cover in the pelagic environment are further suggested by the tendencies of small fish to gather around floating plants and debris (Kingsford, 1993).

The nature of the associations among fish and pelagic coelenterates may change as the fish grow. Juvenile harvestfish, *Peprilus alepidotus*, apparently use their medusa hosts initially for protection from their many vertebrate predators (Mansueti, 1963). As they grow, the harvestfish begin to consume parts of the medusae, and possibly to steal food from the medusae. Fish gut contents and observations indicate that many fish species utilize their pelagic coelenterate hosts for food (reviewed in Mansueti, 1963). These associations generally appear to benefit the fish, while being potentially detrimental to the pelagic coelenterates. The pelagic coelenterates may benefit by removal of amphipod parasites, as documented for whiting and *Cyanea capillata*, and by occasionally consuming fish consorts (reviewed in Mansueti, 1963; Thiel, 1970).

The importance of these associations for either the fish or pelagic coelenterates is unknown. There are few systematic, quantitative data on the frequencies or length of associations. In Mississippi Sound, three species of scyphomedusae occur with several known associated fish species, allowing comparisons among species. *Cyanea capillata* medusae associated with butterfish only, while *Chrysaora quinquecirrha* and *Stomolophus meleagris* medusae were associated with three fish species. Atlantic bumpers (*Chloroscombus chrysurus*) were the most abundant fish consorts, and constituted 82–94% of the fish associated with *C. quinquecirrha* and *S. meleagris* (Table 5). We are not aware of any data on the percentages of the daily rations obtained by either the hosts or consorts from their associates. These associations merge into predation upon the pelagic coelenterates (next section), and the effects are further complicated by the transfer of parasites from the intermediate gelatinous hosts to the definitive fish hosts (last section).

Fish predation on pelagic coelenterates

In addition to predation by pelagic coelenterates on fish, there is also predation by fish on coelenterates. Examination of stomach contents has shown that gelatinous organisms form a portion of the diet of a

Table 4. Associations of fish with scyphomedusae. This table is based on new observations of these associations published since 1978. A large amount of earlier literature is reviewed in Mansueti (1963), Thiel (1970) and Thiel (1978).

Scyphomedusan species	Fish species	Source
Order Coronatae		
Periphylla periphylla	*Icichthys (= Pseudoicichthys)*	Pagès et al. (1996)
(Péron & Lesuer)	*australis* Haedrich	
Order Semaeostomeae		
Aurelia aurita	*Chloroscombrus chrysurus*	Tolley (1987)
	Hemicaranx amblyrhynchus	Tolley (1987)
	Hippocampus zosterae Jordan & Gilbert	Tolley (1987)
	Peprilus paru (Linnaeus)	Tolley (1987)
Aurelia labiata	*Theragra chalcogramma*	Purcell et al. (2000)
Chrysaora achlyos[a]	*Peprilus simillimus* (Ayres)	Martin & Kuck (1991)
Chrysaora melanaster	*Theragra chalcogramma*	Brodeur (1998)
	Zaprora silenus Jordan	Brodeur (1998)
Chrysaora sp.	*Pseudocaranx dentax* (Block & Schneider)	Southcott & Glover (1987)
Cyanea capillata	*Merlangius merlangus* (Linnaeus)	Hay et al. (1990)
	Peprilus triacanthus	Duffy (1988)
	Theragra chalcogramma	Brodeur (1998)
Cyanea lamarcki	*Zaprora silenus*	Brodeur (1998)
Péron & Lesueur	*Merlangius merlangus*	Alvariño (1985), Hay et al. (1990)
	Trachurus trachurus (Linnaeus)	Alvariño (1985)
Cyanea sp.	*Melanogrammus aeglefinus* (Linnaeus)	Koeller et al. (1986)
Desmonema gaudichaudi	*Pseudocaranx dentax*	Southcott & Glover (1987)
(Lesson)	*Trachurus* spp.	Kingsford (1993)
Drymonema dalmatinum	*Caranax crysos* Mitchill	Larson (1987)
Haeckel	*Chloroscombus chrysurus*	Larson (1987)
Order Rhizostomae		
Cassiopea andromeda (Forsskål)	Unidentified fish	Thiel (1979)
Catostylus mosaicus	*Trachurus novaezelandiae* (Richardson)	Southcott & Glover (1987)
(Quoy & Gaimard)	*Trachurus* spp.	Kingsford (1993)
Cotylorhiza tuberculata (Macri)	*Trachurus* sp.	Thiel (1979)
Pseudorhiza haeckeli	*Pseudocaranx dentex*	Southcott & Glover (1987)
Rhopilema nomadica	*Alepes djedaba* (Forsskål)	Spanier & Galil (1991)
Rhizostoma pulmo (Macri)	*Merlangius merlangus*	O'Connor & McGrath (1978)
Thysanostoma thysanura Haeckel	*Caranx* sp.	Thiel (1979)

[a] Martin, Gershwin, Burnett, Cargo & Bloom.

wide variety of fish species. Arai (1988) and Ates (1988) independently published lists of over 50 fish species that consume pelagic coelenterates. As summarized in Arai (1988), much of the earlier evidence for coelenterates in the diets of fish was circumstantial. As ichthyologists become more aware of the necessity of examining fresh fish stomachs, before most gelatinous material is digested or destroyed by preservation, the numbers of known coelenterate eaters is steadily rising. So far, no fish are known for which pelagic coelenterates are the only prey. Some are primarily coelenterate predators, but even they at least eat the hyperiid amphipods associated with the medusae and often also eat salps (Kashkina, 1986; Mianzan et al., 1997). Most fish that eat pelagic coelenterates have broad diets.

A recent study showing the proportion of fish eating pelagic coelenterates is that of Mianzan et al. (1996). They examined over 25 000 stomachs from 69 fish species on the Argentine continental shelf. The

Table 5. Fish species associated with scyphomedusae in the Gulf of Mexico. Numbers are the percentages of each fish species collected by dip net with each jellyfish species, unless otherwise specified (from Tables 1 and 2 in Phillips et al., 1969)

Fish species	*Chrysaora quinquecirrha*	*Stomolophus meleagris*	*Cyanea capillata*	Totals (No.)	Fish size (mm)
Chloroscombrus chrysus	88.2	93.8	0	150	11–39
Peprilus alepidotus	5.9	5.5	0	9	14–38
Caranx sp.	5.9	0	0	2	18
Peprilus burti Fowler	0	0	100	30	6–34
Stephanolepis hispidus (Linnaeus)	0	0.8	0	1	17.5
Total fish (No.)	34	128	30	192	–
Total jellyfish (No.)	27	191	39	257	–
Jellyfish with fish (%)	53	10	72	–	–
Jellyfish size (mm)	25–110	60–130	30–130	–	–

abundance of ctenophores, the predominant coelenterate group, was greatest during the spring. During that period, over 28% of the stomachs, belonging to 35% of the fish species, included at least some ctenophores. During the remainder of the year, these values fell to 7–17% of the stomachs, and 15–23% of the fish species. Two stromateoid fish, *Stromateus brasiliensis* Fowler and *Seriolella porosa* Guichenot, fed almost exclusively on ctenophores most of the year, and one scorpaenid fed primarily on ctenophores during the spring and summer.

Because there are no quantitative data on the passage times of gelatinous prey in fish guts, it is not possible to convert data on stomach contents to feeding rates. Nevertheless, it is possible to predict that, unless such digestion rates vary greatly with specific fish or prey, predation by the large numbers of species of fish with generalized diets is more ecologically important than the predation by the relatively small numbers of specialized fishes with primarily gelatinous diets.

Harbison (1993) points out that the suborder Stromateoidei includes the group of fishes for which we have the most extensive evidence of specialized feeding on salps or pelagic coelenterates. As in the Mianzan et al. (1996) study, species of the family Centrolophidae and the family Stromateidae are particularly well documented as extensive coelenterate feeders. The latter family includes such prized human food fishes as the butterfish *Peprilus triacanthus*.

On the other hand, pelagic coelenterates form portions of the diets of a broad range of such common and commercially important species as spiny dogfish, *Squalus acanthias* Linnaeus, chum salmon, *Onco-*

rhynchus keta (Walbaum), sablefish, *Anoplopoma fimbria* (Pallas), and various gadoids, scorpaenids and scombrids (Arai, 1988; Brodeur & Pearcy, 1992). Early work on the spiny dogfish rarely found pelagic coelenterates in the diet; however, when measurements were made of fresh specimens at sea, pelagic coelenterates represented 30–40% by volume of the stomach contents (Bowman et al., 1984; McFarlane et al., 1984). More recently, Brodeur & Pearcy (1992) found the By-the-Wind Sailor, *Velella velella,* (Linnaeus) to be a major food item when available off Oregon, and Ellis et al. (1996) found ctenophores in the diet of dogfish in the Irish Sea.

Salmon are the dominant intermediate level predators in the upper 50 m of the North Pacific. There is a good deal of overlap in the generalist diets of the six species, however, chum salmon differ in also utilizing gelatinous prey. As shown by a number of Russian, Japanese, Canadian and American scientists, the diet varies with fish age, and among years and localities from primarily arthropod, to primarily gelatinous. On the high seas, the gut contents of fresh caught chum juveniles is often an amorphous mass of white or red jelly that is difficult to identify but may include the hydromedusan, *Aglantha digitale* (O. F. Müller), and hyperiid amphipods, which are frequent associates of gelatinous animals (Tsuruta, 1963; Davis et al., 1998). Inshore, other medusae and ctenophores may be utilized (Black & Low, 1983; Healey, 1991). This partially gelatinous diet may reduce competition with the other salmon species (Azuma, 1992, 1995; Tadokoro et al., 1996).

In midwater, pelagic coelenterates are found in the diets of lantern fish (family Myctophidae), grenadiers (family Macrouridae), slickheads (family Alepocephalidae) and deep sea smelts (family Bathylagidae) (Arai, 1988; Carrasson & Matallanas, 1990; Beamish et al., 1999). The myctophid, *Stenobrachius leucopsarus*, is the dominant species in the midwater community of the subarctic Pacific. The stomach contents include up to 12% cnidarians and ctenophores depending on location (Beamish et al., 1999). Also in locations of the Pacific Ocean and neighboring seas, for deep-sea smelts such as *Bathylagus ochotensis* Schmidt and *Leuroglossus schmidti* Rass, pelagic coelenterates may form up to 30% and 41%, respectively, of the stomach contents (Beamish et al., 1999).

Fish may show physical adaptations to a gelatinous diet. Harbison (1993) noted that primarily medusivorous fish, such as the stromateoid species, typically have deep bodies and underslung jaws, however, fish that include a significant proportion of pelagic coelenterates in generalized diets may be much more streamlined. For example, the beautifully streamlined chub mackerel, *Scomber japonicus* Houttuyn, of the Pacific or the very similar Atlantic mackerel, *S. scombrus* Linnaeus, can feed either by filter feeding using the gill rakers, or by individual selection of organisms. In the laboratory, Atlantic mackerel select individuals of the hydromedusan, *Aglantha digitale*, in preference to filtering copepods (Runge et al., 1987).

Better correlated than body shape with a gelatinous diet is an enlarged digestive tract. Harbison (1993) summarizes work by Buhler (1930) and later workers indicating the stromateoid fishes have both exceptionally large stomachs and extremely long intestines. The lumpfish, *Cyclopterus lumpus* Linnaeus, which eats the ctenophore *Pleurobrachia* sp., has a large stomach and a narrow moderately long intestine (Eggeling, 1908).

Of interest is the variation in digestive tract structure within the salmon of the North Pacific. In keeping with their partially gelatinous diet, chum salmon have enlarged stomachs compared with the other species of *Oncorhynchus* (Welch, 1997). The stomach is a large bag-like structure that nearly fills the coelomic cavity and is formed of a thick, soft tissue lacking the muscle tone evident in the five other species. The chum stomach is capable of holding approximately 3.5-times the volume of other species at equivalent body lengths. Chum do not have an enlarged or lengthened intestine.

Fish feeding on gelatinous species also may have pharyngeal or oesophageal modifications, presumably to prevent regurgitation. *Mola mola* Linnaeus has three rows of recurved pharyngeal teeth (Suyehiro, 1942). In the stromateoid fishes, there are oesophageal sacs with denticulate papillae (Gilchrist, 1922; Isokawa et al., 1965). *Genicanthus personatus* Randall, the masked angelfish, includes hydromedusae and siphonophores in its diet and has finger-like oesophageal papillae that point posteriorly (Howe, 1993). The oesophagus of chum salmon is strongly muscular with a well-defined sphincter (Azuma, 1992).

Pelagic coelenterates display a variety of characteristics and behaviors that might be effective in reducing fish predation. The stinging nematocysts of cnidarians presumably deter some potential fish predators. Cnidae are released by the scyphomedusan, *Stomolophus meleagris*, when pinched to simulate a predator attack (Shanks & Graham, 1988). These cnidae drive off the associated juvenile fish and could potentially also affect larger fish predators. Some planktonic coelenterates respond to stimulation by 'crumpling' or escape behaviors (Mackie, 1995). It is unclear how crumpling would deter a visual predator, but a vigorous escape response such as that of *Aglantha digitale* might reduce the frequency of capture. There is no direct proof that transparency reduces predation, although its prevalence in gelatinous animals suggests that is of considerable survival value (Johnson & Widder, 1998). Conversely, the loss of transparency upon disturbance in the siphonophore, *Hippopodius hippopus* (Forsskål), has been hypothesized as a predator deterent (Mackie, 1995). Bioluminescence occurs in all known genera of ctenophores, except *Pleurobrachia*, is widespread among pelagic hydrozoans, and is found in some scyphomedusae (Widder et al., 1989; Haddock & Case, 1995; Mackie, 1995; Arai, 1997). Its prevalence and the elaborate displays suggest that bioluminescence is of great value in detering visual predation. While octocorals may contain chemicals which are unplatable or cause vomiting in fish (e.g. Gerhart & Coll, 1993), and hydroid polyps may contain metabolites that are unpalatable (Stachowicz & Lindquist, 1997), similar compounds have not yet been identified in pelagic cnidarians or ctenophores.

Since pelagic coelenterates are utilized not only by the small number of specialist fish feeders but by large numbers of species with more generalized diets, this predation is probably of ecological importance. Arai (1988) summarizes data on the caloric content of pelagic coelenterates and speculates on their dietary

value to the fish. As noted above, it is not possible to calculate field based feeding rates of fish from observed stomach contents since digestion rates are lacking. In turn, without field based feeding rates, it is also not possible to quantitatively evaluate the importance of fish predation on pelagic coelenterates in marine food webs. A single paper, Oviatt & Kremer (1977), combines laboratory measurements of feeding rates by American butterfish, *Peprilus triacanthus*, on the ctenophore, *Mnemiopsis leidyi*, with population abundances in Narragansett Bay and estimated possible predation rates of 5–15% d^{-1}. These subjects will not advance greatly until digestion rates become available and allow calculation of field based feeding rates.

It is to be expected that if the population of a fish species that feeds on pelagic coelenterates decreases, the prey species may increase in numbers. In spite of the lack of quantitative data on predation rates as discussed above, there are instances where overfishing of a predator is believed to have contributed to increases of pelagic coelenterate populations. Historically Atlantic mackerel, *Scomber scombrus*, did not reproduce in the Black Sea, but there were massive migrations from the Sea of Marmara onto the Northwestern Shelf of the Black Sea in most years. Mackerel had disappeared as a commercial species of the Black Sea by the end of the1960s (Caddy, 1993). As noted above, mackerel are known predators of pelagic coelenterates (Scott, 1914, 1924; Runge et al., 1987). Zaitsev & Polischuk (1984) suggest that the increase of *Aurelia aurita* in the Black Sea in the 1970s and 1980s was due, at least in part, to decreased autumn predation by the mackerel (see also Zaitsev, 1992). In the Adriatic Sea, a population increase of the scyphomedusan, *Pelagia noctiluca*, was correlated with increased catch of several predator fish in the late 1970s (Avian & Rottini-Sandrini, 1988). This led to proposals that overfishing was decreasing these predators and allowing the *P. noctiluca* bloom (Avian & Rottini-Sandrini, 1988; Legović, 1991; Parsons, 1995). However, in this case, Vućetić & Alegria-Hernandez (1988), in a more extensive analysis of similar data, concluded that other factors were increasing the populations of both fish and jellyfish. Overfishing can not explain either the occurrence of a past bloom of *P. noctiluca* in the Adriatic Sea 1910–1914 or its precipitous decline in 1986 following the 1976 bloom (see references cited in Purcell et al., 1999a).

Pelagic coelenterates as intermediate hosts for parasites of fish

Trematode, cestode and nematode larvae are widely distributed in pelagic Hydrozoa, Scyphozoa and Ctenophora (Lauchner, 1980a, b). It is not known to what extent fish acquire the parasites by eating coelenterates rather than eating other possible intermediate hosts. As knowledge expands on inclusion of gelatinous species in marine fish diets, there is also increasing awareness of the probable role of coelenterates in the transmission of helminth (metazoan worm) parasites to fish (Arai, 1988; Marcogliese, 1995).

Digenetic trematodes are the most thoroughly investigated parasites of pelagic coelenterates and fish. Larval stages of genera such as *Opechona* and *Neopechona* in the family Lepocreadiidae include cercariae, which develop into rediae in gastropods, followed by metacercariae that develop in medusae, ctenophores or other intermediate hosts. Metacercariae have been found in several hydromedusae, such as *Aglantha digitale* (see Koie, 1975; Martorelli, 1996, 2001) and in ctenophores, such as *Pleurobrachia pileus* (see Yip, 1984). The definitive hosts, where the trematode becomes sexually mature, are fish, such as mackerel, which are known to eat pelagic coelenterates. Similar life cycles with mollusc, coelenterate and fish hosts have been demonstrated in the family Hemiuridae for species of *Lecithocladium* (see Koie, 1991), and in the family Fellodistomidae for species of *Monascus* (see Girola et al., 1992; Martorelli & Cremote, 1998).

The rates of natural infections of other zooplankton intermediate hosts with fish parasites are usually very low (Marcogliese, 1995). In the few cases so far investigated, the rates of infections of hydromedusae and ctenophores with trematodes may be higher than for other zooplankton, but vary with location, season or host size. For example, in hydromedusae (1670 specimens of *Phialidium* sp. and 1892 *Liriope tetraphylla* (Chamisso & Eysenhardt)) examined from the Argentine-Uruguayan Common Fishing Zone, the prevalences of *Monascus filiformis* (Rudolphi) were 16–39% and 2–25% respectively, in three collecting zones (Girola et al., 1992). In *Pleurobrachia pileus* from Galway Bay, Ireland, prevalences of *Opechona bacillaris* Mokin showed maxima of up to 50% in early summer but no infection in mid-winter (Yip, 1984). No infections were found in *P. pileus* less than 1 mm in length.

Adult nematodes (Ascaridoidea, Anisakidae) of the genus *Hysterothylacium* are very widely distributed in marine fish. Coelenterates are among the wide variety of planktonic and benthic invertebrates that may serve as intermediate hosts. *Hysterothylacium* larvae have been recorded in hydromedusae, such as *Aglantha digitale* (see Svendsen, 1990) and in the ctenophores, *Pleurobrachia pileus* and *Mnemiopsis leidyi* (see Svendsen, 1990; Koie, 1993; Gaevskaya & Mordvinova, 1993; Mutlu & Bingle, 1999). Although cestodes have been recorded in coelenterates, the larvae are difficult to identify and no life cycles involving coelenterates have been established as yet.

Discussion

This paper describes what is known about the interactions between pelagic coelenterates and fish. The interactions can be either positive or negative in their potential effects on the commercially important fish populations, which are of particular interest. The negative interactions include predation by pelagic coelenterates on fish eggs and larvae, for which considerable quantitative data exist, potential competition for food, and transmission of parasites from pelagic coelenterates to fish, however, the ultimate effects of these interactions on fish populations are unknown in most cases. On the other hand, fish may benefit from predation on pelagic coelenterates and from commensal relationships between young fish and medusae. Again, data are lacking to evaluate the magnitude and dietary importance of fish predation on pelagic coelenterates, or whether young fish of some species are dependent on medusae for survival.

With the poor understanding of the importance of these interactions, it obviously is difficult to assess the effects of predicted changes in climate, eutrophication or over fishing on pelagic coelenterate populations and their interactions with fish. Climate changes may have various effects. For example, release of medusae by hydroids and scyphistomae depends on light, temperature, salinity, and feeding (Arai, 1992, 1997; Purcell et al., 1999b). These environmental factors could change the timing and abundance of pelagic coelenterates and ichthyoplankton and alter the predation effects (e.g. Table 2). Eutrophication, which may decrease biodiversity but increase some holoplanktonic and estuarine species especially in coastal waters, is discussed by Arai (2001).

Over fishing has dramatically altered fish populations around the world, not only in numbers but also in trophic structure. Fisheries typically first have concentrated on the large, long-lived, piscivorous fish and gradually are turning to small, planktivorous fish (Pauly et al., 1998b). The extent of this concentration on fishing high trophic levels shows wide regional variation (Caddy et al., 1998; Pauly et al., 1998a). Also, the distinction between piscivorous and planktivorous fish is often not clear. Nevertheless, it is interesting to speculate on what effects this fishing may have on the trophic structure of marine ecosystems and particularly on the pelagic coelenterate populations.

Characteristics of gelatinous zooplankton allow them to quickly exploit new resources in changing circumstances (Alldredge, 1983). Many pelagic coelenterates increase their populations very rapidly through a combination of high growth rates, and sexual plus asexual reproduction, whereas fish lack the abilities to asexually multiply and to have several generations in one season. Greve & Parsons (1977) suggest a dichotomy in which two pathways might exist for the transfer of energy up the marine food web leading alternatively to fish or pelagic coelenterates. In waters with low productivity, nanophytoplankton (e.g. small flagellates), small zooplankton and zooplanktivorous ctenophores or medusae would predominate, and alternatively, in highly-productive waters, microphytoplankton (e.g. large diatoms), large zooplankton and zooplanktivorous fish would predominate. This oversimplified dichotomy has been criticized by Longhurst (1985) because pelagic coelenterates also utilize larger particles including fish, by Arai (1988) because pelagic coelenterates are not necessarily the top predators, but are eaten by a variety of predators from chaetognaths to birds, and by Mills (1995) because pelagic coelenterates are also abundant in areas of high productivity.

More recently, Parsons (1992, 1995) summarizes several possible effects of removal of top pelagic fish predators, and suggests that pelagic coelenterates may supplant many commercial fish species as top predators. It is unlikely that many pelagic coelenterates will replace piscivorous fish in marine food webs. Diets primarily of larval or juvenile fish are confined to a few cnidarian species such as cystonect siphonophores and some cubomedusae (Larson, 1976; Purcell, 1997). Most predation on fish eggs and larvae by pelagic coelenterates is by species with broad diets. Most pelagic coelenterates consume primarily zooplankton, and would be expected to compete with zooplanktivorous

fish such as anchovies, herring and sardines. When over fishing includes those fish species, there could be significant unconsumed zooplankton, and pelagic coelenterate populations might expand (Caddy, 1993). Even then, the outcome is unclear because many pelagic coelenterate populations can be controlled by predation by other gelatinous species (Purcell, 1997; Purcell et al., 2001).

As discussed above, commercial removal of fish predators of pelagic coelenterates also could allow their populations to increase. Many prized commercial fish, such as chum salmon, mackerel and Atlantic butterfish, consume pelagic coelenterates as well as fish and zooplankton. Again, predation by other pelagic coelenterates might prevent the populations from expanding in response to the removal of fish predators.

It is not possible to predict the final ecosystem balances from over fishing, given the present shortage of information. In combination with the effects of climate change and eutrophication, ecosystem changes may vary widely among locations. It is obvious that further research is essential.

Acknowledgements

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